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Systematics and Phylogeny of *Philine* (Gastropoda: Opisthobranchia), with Emphasis on the *Philine aperta* Species Complex

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Abstract. This study includes detailed morphological examination of 16 species of *Philine* to reconstruct a phylogenetic hypothesis of relationships within the Philinidae. Our purpose is to test the monophyly of a complex of species that closely resemble the type species, *Philine aperta* (Linnaeus, 1767). Our cladistic analysis of *Philine* supports both the monophyly of the genus and of a subclade of the *Philine aperta* clade. This *P. aperta* subclade consists of highly derived species that serve as poor models for understanding plesiomorphic attributes within the genus *Philine* and also within the family Philinidae; aspects of their morphology are too highly modified to provide appropriate exemplars of evolution of the entire clade. The systematics of this subclade has long been confused because of only subtle, but consistent, differences between species. Consequently, species have been synonymized and separated repeatedly. We found several characters of systematic importance that had not been used previously, including microstructure of the gizzard plates, fine details of the penial papilla, and branching of the prostate complex. We describe each of the taxa in the *P. aperta* clade that we examined, including the first detailed description of *Philine orientalis* A. Adams, 1854, and the first anatomical description of *Philine elegans* Bergh, 1905. We also describe four new species in the *Philine aperta* clade: *Philine fenestra* sp. nov., *Philine paucipapillata* sp. nov., *Philine puka* sp. nov., and *Philine sarcophaga* sp. nov. Specimens identified as *Philine orientalis* A. Adams, 1854 from Hong Kong (Morton & Chiu, 1990) and Cambodia (present study) are morphologically distinct from those found elsewhere (present study) and represent a distinct species described here as *P. paucipapillata* sp. nov. Lastly, we redescribe *Philine alba* Mattox, 1958, from California and differentiate it from the specimens of *P. alba* from several localities in the Western Atlantic described by Marcus & Marcus (1967) and Marcus (1974). We erect the name *P. alboides* sp. nov. for the Marcuses' specimens.

INTRODUCTION

The genus *Philine* Ascanius, 1772 contains at least 90 species, not including synonyms (Rudman, 1972b), making it among the most species-rich genera of opisthobranchs. The systematic boundaries of many species and nominal genera have been the source of considerable confusion; this confusion is exacerbated by several of these species having been recently introduced by international shipping, probably through discharge of ballast water (Gosliner, 1995; Gosliner & Williams, 2007). It is imperative to have reliable systematic and morphological data available both to resources managers and systematists.

Unfortunately, most species are known only from their shells. This has created considerable taxonomic confusion and misidentifications of taxa, owing to the convergent shell morphology within this group. Species with similar shells often have dramatic differences in internal anatomy. For example, there has been confusion surrounding the identity of the two large, shallow-water species that have been introduced into San Francisco Bay (Gosliner, 1995; Rudman, 1998b; Gosliner & Williams, 2007). Recently, one of our colleagues, who has considerably more experience in studying details of shell structure, misidentified shells of one introduced species as *Philine argentata* Gould, 1860 despite the fact that this species has gizzard plates that are radically different from those of the species he was considering. So strong is convergence in shell morphology between taxa that it cannot be considered by itself to constitute a reliable basis for differentiating species. Although shell characters are informative to a degree, we strongly discourage the practice of basing new taxa exclusively upon shell morphology, because it further exacerbates the systematic confusion within this diverse group of species. Presently, fossil taxa cannot be included in an analysis of fine-level species differences because other key morphological features are unknown.

Despite the challenges associated with using shell characters in this group, the anatomy remains unknown for the majority of known *Philine* species. Many morphological descriptions of *Philine* species have been undertaken over the past several decades (Marcus & Marcus, 1966, 1967, 1969; Rudman, 1970, 1972a, b; Gosliner, 1988), and these studies describe new taxa and review the anatomy of previously identified species. In one of these studies, Guiart (1901:107;fig. 59) presents an excellent drawing of the overall anatomy and body plan of *Philine* with his depiction of the anatomy of *Philine quadripartitia* (as *P. aperta*). Still, the anatomy is known only from approximately one third of the identified species of *Philine*. This difficulty precludes a monographic review that studies the majority of *Philine* species. Thus, this article is not a monographic review of *Philine*, nor is it meant to be a comprehensive test of the monophyly of all generic names applied to taxa within the Philinidae. Such work is not possible at this time, because many of the type species are known only from shells and cannot be studied in a comprehensive phylogenetic analysis.

We find that, within *Philine*, most of the systematically informative variation is internal; the external features have been considered uniform throughout the genus. Most animals are white. The body is composed of cephalic and posterior shields flanked by relatively narrow parapodial lobes. Interspecific variations of the gizzard plates, penis and prostate complex, shell structure and sculpture, and radular formula have been used as criteria for subdividing the genus (Lemche, 1948; Habe, 1950; Marcus, 1974), but none of these criteria have been tested with a cladistic framework. Consequently, many of the genera are monotypic, do not divide the genus into monophyla, and are not accepted by other authors (Rudman, 1972b; Gosliner, 1988).

This article consolidates the current state of knowledge for the external and internal anatomy of well-described species of *Philine* to identify well-defined clades to begin recognizing well-supported groups so that future studies can refine *Philine* systematics. We focus on the anatomy of species that are members of the *Philine aperta* species complex, in which the prostate gland has complex secondary branching and the gizzard plates are ornamented with pores or other structures. As we embarked on this study, we found that subtle and consistent differences in anatomy do exist among species in the *P. aperta* species complex that had been synonymized previously. After conducting a phylogenetic analysis that includes all the known members of this complex and 11 additional species in the genus, we found that these subtleties are synapomorphies that confirm that the *P. aperta* species complex is a clade. The taxa included in the analysis represent the entire known range of anatomical variation within *Philine*. In addition, two outgroup taxa, *Scaphander mundus* Watson, 1883 and *Cylichna alba* (Brown, 1827) were included.

This article also describes several new species and constructs a preliminary phylogenetic hypothesis to determine monophyly of *Philine* and clades within the Philinidae.

MATERIALS AND METHODS

Material examined: The material examined is deposited at the following institutions: California Academy of Sciences, San Francisco, California, USA (CASIZ); The Natural History Museum, London, United Kingdom (BMNH); Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM); Iziko South African Museum, Cape Town, South Africa (SAM); and the Museum National d'Histoire Naturelle, Paris, France (MNHN).

Morphological study: We begin by discussing the type species, *P. aperta*, and the rest of the species are discussed and arranged alphabetically by species name. Features of living animals were recorded from photographs and notes by collectors. The specimens were dissected by ventral and dorsal incision to facilitate morphological examination. The internal features were examined using a dissecting microscope and drawn with the aid of a camera lucida. Special attention was paid to the morphology of the reproductive system, including the detailed anatomy of the penial papilla and prostate. The buccal mass was dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. Gizzard plates were removed by dissection and rinsed in deionized water, dried, and mounted on electron microscopy stubs. The radula was then also rinsed in water, dried, and mounted for examination by scanning electron microscopy (SEM). In addition to anatomical information collected by direct examination of specimens during this study,

Table 1
Literature used to study *Philine* species included in our phylogenetic analysis

Species	Literature
P. alba Mattox, 1958	Mattox, 1958; Marcus and Marcus, 1967; Marcus, 1974; present study
P. "*alba*" (called *P. alboides* herein)	Marcus and Marcus, 1967; Marcus, 1974; present study
P. angasi (Crosse & Fischer, 1865)	Rudman, 1970, 1972a, 1998b; present study
P. aperta (Linnaeus, 1767)	Bergh, 1907; Brown, 1934; Hurst, 1965; Marcus and Marcus, 1966; Horikoshi, 1967; Marcus, 1974; Thompson, 1976; present study
P. argentata Gould, 1860, a synonym of *P. orientalis*	Habe, 1950; Morton and Chiu, 1990; Higo et al., 1999; present study
P. auriformis Suter, 1909	Rudman, 1970, 1972a, b; Gosliner, 1995; present study
P. babai Valdés, 2008	Valdés, 2008; present study
P. berghi E. A. Smith, 1910	Bergh, 1907; O'Donoghue, 1929
P. elegans Bergh, 1905	Bergh, 1905; present study
P. falklandica Powell, 1954	Rudman, 1972a; present study
P. fenestra Price, Gosliner, and Valdés, n. sp.	Present study
P. finmarchica Sars, 1858	Lemche, 1948; Marcus and Marcus, 1969; Marcus, 1974; present study
P. gibba Strebel, 1908	Marcus and Marcus, 1969; Rudman, 1972a; Seager, 1978; present study
P. habei Valdés, 2008	Valdés, 2008; present study
P. infundibulum Dall, 1889	Marcus and Marcus, 1967; Marcus, 1974; present study
P. lima (Brown, 1825)	Lemche, 1948; Marcus and Marcus, 1969; present study
P. orca Gosliner, 1988	Gosliner, 1988; Baba, 1990
P. "*orientalis*" A. Adams, 1854, called *P. paucipapillata* herein	Morton and Chiu, 1990; present study
P. pruinosa (Clark, 1827)	Lemche, 1948; Thompson, 1976; Morton and Chiu, 1990
P. puka Price, Gosliner, and Valdés, n. sp.	Present study
P. quadrata (Wood, 1839)	Lemche, 1948; Horikoshi, 1967; Marcus and Marcus, 1969; Rudman, 1972a; Thompson, 1976; present study
P. quadripartita (Ascanius, 1772)	Bergh, 1901, 1905; Brown, 1934; Hurst, 1965; Horikoshi, 1967; Thompson, 1976; present study
P. rubrata Gosliner, 1988	Gosliner, 1988; Baba, 1990
P. sarcophaga Price, Gosliner, and Valdés, n. sp.	Present study
P. t. thurmanni Marcus and Marcus, 1969	Marcus and Marcus, 1969
S. kensleyi Gosliner, 1988	Gosliner, 1988
C. alba (Braun, 1827)	Lemche, 1956
S. mundus Watson, 1833	Marcus and Marcus, 1966; Marcus, 1974

morphological data were augmented by prior publications on the anatomy of species of *Philine* (Table 1).

Phylogenetic analysis: To calculate the most parsimonious phylogenetic trees, data were analyzed with Phylogenetic Analysis Using Parsimony (PAUP*), version 4.0b10 (Swofford, 2002), by using the heuristic algorithm (Branch swapping option [TBR]). In cases in which a taxon had two states for a given character, they were treated as uncertain. Both the accelerated transformation (ACCTRAN) and the delayed transformation (DELTRAN) optimizations were used for character transformation. In both cases, the analyses were performed treating the characters as unordered. One thousand random starting trees were obtained via stepwise addition. The trees were rooted using *C. alba* and *S. mundus* as outgroups. In successive analyses, each outgroup taxon was used as the only outgroup, and in other analyses both taxa (*C. alba* and *S. mundus*) were used as an outgroup. The resulting trees did not vary in topology. Both of these taxa have several attributes (such as a less detorted body and a more well-developed shell) that suggest that they are more plesiomorphic in many aspects of their anatomy, and they are thought to be close basal relatives of the philinids (Mikkelsen, 1996). A decay analysis using a heuristic search by PAUP* was conducted to estimate branch support. Synapomorphies were mapped using the character trace option in MacClade 4.08 (Maddison & Maddison, 2005) based on the strict consensus tree from the PAUP* analysis.

SPECIES DESCRIPTIONS

Family PHILINIDAE Gray, 1850

Philine Ascanius, 1772:329.

Type species: *Bulla aperta* Linnaeus, 1767 by monotypy.

Diagnosis: Divided body consisting of cephalic and posterior shields. Posterior shield contains internalized shell. Distinct parapodial lobes (Figure 1A). Jaw rodlets absent. Radular formula 0–6.1.0–1.1.0–6. Rachidian tooth reduced or absent. Inner lateral teeth usually denticulate. Gizzard plates three, equal or unequal in size, that are not covered by muscles (Figure 1B). Reproductive system monaulic. Ciliated sperm groove along right side. Penis simple or complex. Euthyneurous nervous system with elongate visceral loop.

Philine aperta (Linnaeus, 1767)

(Figures 2A, B; 3; 4)

Bulla aperta Linnaeus, 1767:1183.
Philine aperta (Linnaeus, 1767) Bergh, 1907:24, pl. 5, figs. 5–10.
Bullaea capensis Pfeiffer, 1840. Bergh, 1907:24.
Bulla schroeteri Philippi, 1844:94, pl. 20, fig. 2; Bergh, 1907:24.
Philine capensis O'Donoghue, 1929:10.
Philine aperta guiniensis Marcus and Marcus, 1966:159, figs. 9–18. Marcus, 1974:360, fig. 104.

Material: SAM A54287, University of Cape Town Ecological Survey, Station NAD 75, one specimen, 30 mm, coarse sand, 38 m depth, 29°19.8′S, 31°26.2′E, September 10, 1964. SAM A54286, University of Cape Town Ecological Survey, Station NAD 59B, one specimen, dissected, 42 mm, green mud, 77 m depth, 29°26′S, 31°46.2′E, September 9, 1964. SAM, University of Cape Town Ecological Survey, Station FAL 786 L, one specimen, dissected, 20 mm, coarse sand and shell, 27 m depth, 34°17.0′S, 18°29.2′E, February 15, 1965. SAM, University of Cape Town Ecological Survey, Station FAL 743 Q, one specimen, 9 mm, coarse sand and shell, 7 m depth, 34°09.5′S, 18°50.6′E, February 16, 1965. SAM, University of Cape Town Ecological Survey, Station FB 402A, False Bay, South Africa, two specimens, 6–9 mm, fine sand, 31 m depth, 34°8.8′S, 18°33.5′E, May 16, 1961. SAM A54288, University of Cape Town Ecological Survey, Station SCD 189D, False Bay, South Africa, three specimens, 2 dissected, 40–60 mm, fine sand, 10 m depth, 34°05.8′S, 23°23.2′E, November 29, 1960.

Distribution: Known from Saldanha Bay (South Africa) to Mozambique.

Natural history: This species is found in relatively shallow water from 3 to 100 m depth in coarse sandy substrate. The egg masses (Figure 2B) are elongate sacs that are attached to the sand by a mucous thread.

External morphology: The living animal is uniformly white to yellowish (Figure 2A), ranging in size from approximately 1 to 6 cm. The cephalic shield is longer than the posterior shield (Figure 3A). The parapodial lobes are thick and muscular, and the posterior notch is shallow.

Internal morphology: The shell is relatively tightly coiled, and its surface lacks sculpture.

There is a single, short, ventral oral gland, and there are two dorsal oral glands. The buccal bulb and radula are reduced; the radular formula is 16–20 × 1.0.1 The inner lateral tooth is broad with 37–51 denticles (Figure 4C). The crop is indistinct. Although the gizzard is muscularized, the plates are not covered with muscles. The esophagus passes directly through the three large gizzard plates. The plates are spindle-shaped, and each has two medium-sized pores (Figure 4A, B). The paired plates (e.g., Figure 4A) are larger than the unpaired plate (Figure 4B). The gizzard-plate microsculpture consists of circular indentations, within which there is a finely meshed subsculpture (Figure 4D). The salivary glands are short.

The fused pleural-parietal ganglion can be adjacent to or can adjoin the anterior supraintestinal ganglion. The genital ganglion is fused to the visceral ganglion. The subintestinal ganglion is adjacent to the fused visceral and genital ganglia.

The penial papilla is hammer-shaped with subequal lobes, fitting within the penial sac without distending it (Figure 3B). The convoluted prostate branches to the ejaculatory duct, and a short muscle connects the end of the prostate to the sac (Figure 3C). The ejaculatory duct is short.

The convoluted ampulla narrows to the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figure 3D). The mucous gland is large, and it bends at the free end. There is a secondary bursa copulatrix at the base of the spherical, thin-walled, primary bursa copulatrix.

Discussion: The gizzard plates of *P. aperta* are shaped like "tricornered hats" (Marcus, 1974:347) with medium-sized pores. These plates look most similar to those in *Philine orientalis*, *P. quadripartita*, and especially *Philine paucipapillata*. The plates of *Philine angasi* and *Philine elegans* are similar, but they are also twisted, and more concave. *Philine puka* also has plates with the tricornered hat shape, but it has large pores. The gizzard-plate microstructure is most like that in *P. angasi* and *P. paucipapillata*.

The penial morphology of *P. aperta* is distinct because of the wide penial sac and the three long lobes. The hammer head is closely appressed to the anterior of the sac. It is most similar in shape to the hammer heads of *P. orientalis* and *P. quadripartita*.

The narrow posterior portion of the cephalic shield is similar to that of *Philine angasi*, *P. argentata*, *P. orientalis*, *P. paucipapillata*, and *P. puka*.

Bergh (1901) and Lemche (1948) synonymized the European *P. quadripartita* with the African *P. aperta*. Marcus & Marcus (1966) distinguished between the

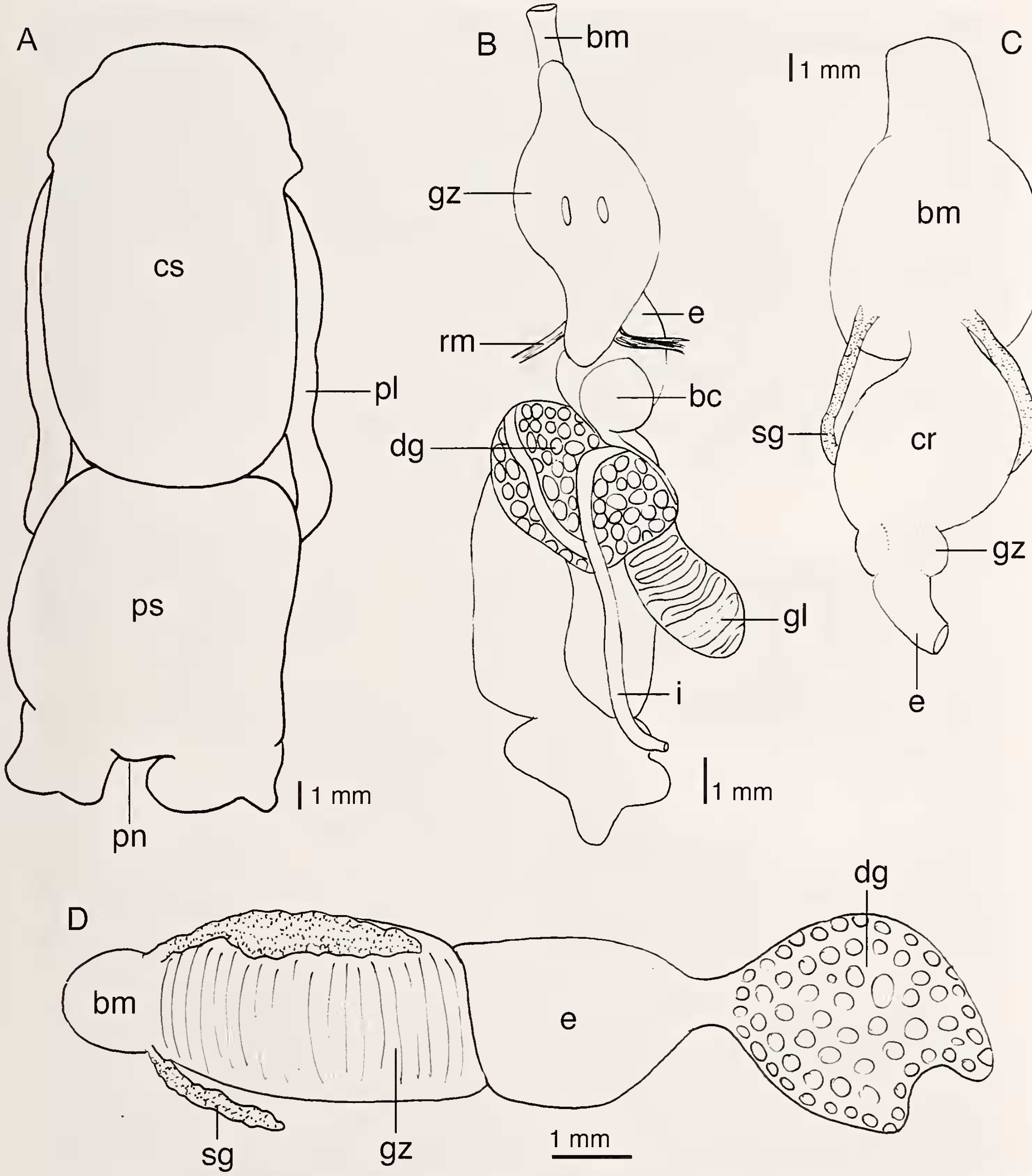

Figure 1. General external morphology and anatomy of species of *Philine* showing the main characteristics of this group and comparing the digestive system of three species. Additional information on the general anatomy can be found in Guiart (1901:107, fig. 59). **A**, dorsal view of a specimen of *P. auriformis* (CASIZ 097499), showing the cephalic shield (cs), posterior shield (ps), parapodial lobes (pl), and posterior notch (pn); **B**, digestive system of *P. puka* (CASIZ 082128), showing that the gizzard plates are typically not covered by muscles (gz); **C**, anterior portion of the digestive system of *P. alba* (CASIZ 076681), showing the small, nonmuscularized gizzard (gz); **D**, digestive system of *P. infundibulum* (CASIZ 076159), showing the muscularized gizzard with the gizzard plates covered with muscles (gz). Abbreviations: **bc**, bursa copulatrix; **bm**, buccal mass; **cr**, crop; **cs**, cephalic shield; **dg**, digestive gland; **e**, esophagus; **gl**, gill; **gz**, gizzard; **i**, intestine; **pl**, parapodial lobe; **pn**, posterior notch; **ps**, posterior shield; **rm**, retractor muscle; **sg**, salivary gland.

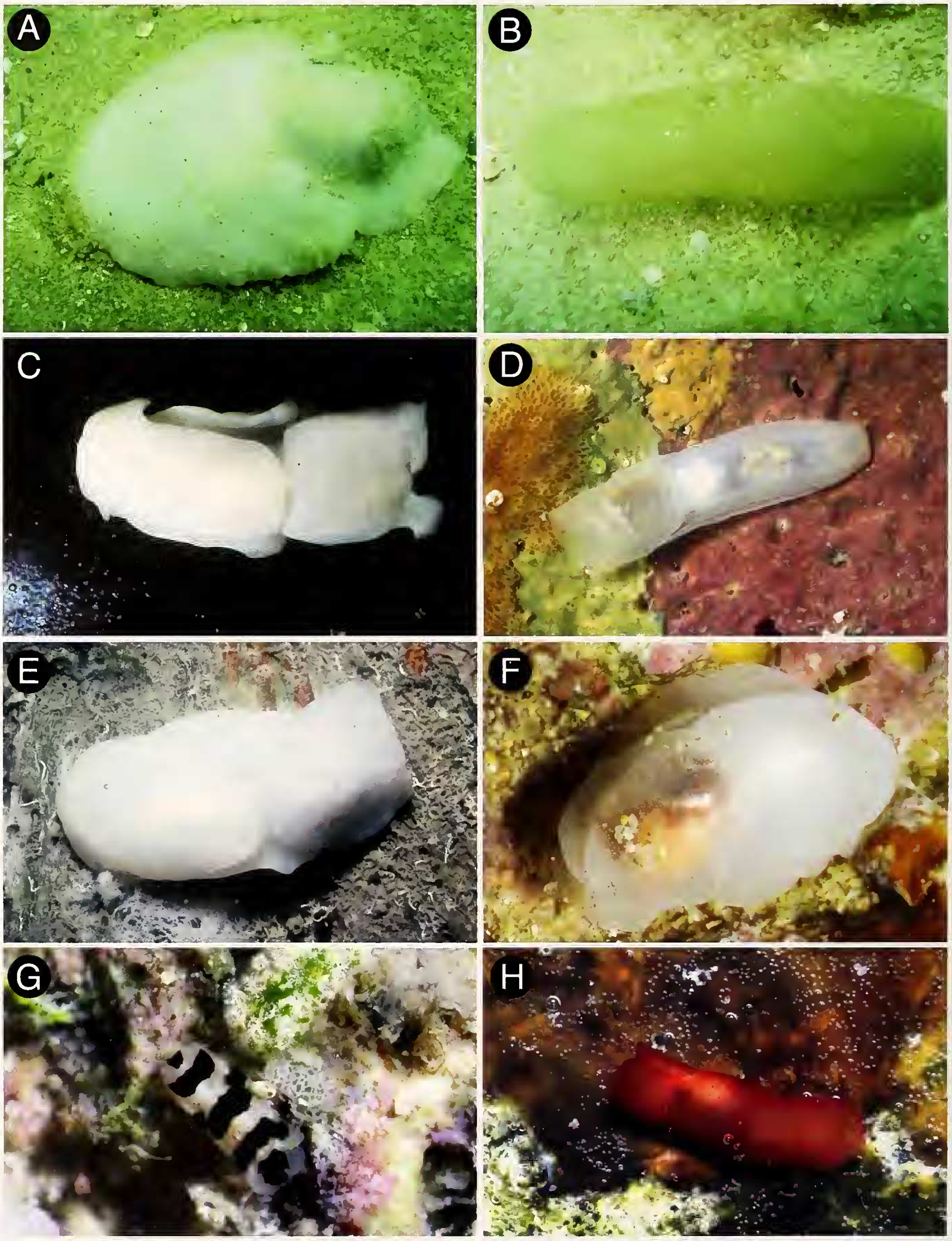

Figure 2. Photographs of living animals: **A,** *P. aperta*, Long Beach, False Bay, Cape Town, South Africa; **B,** *P. aperta*, egg mass, Long Beach, False Bay, Cape Town, South Africa; **C,** *P. auriformis*, Bodega Harbor, California; **D,** *P. elegans*, Mabini, Batangas, Luzon, Philippines; **E,** *P. orientalis*, Matiara Hotel, Langkawi Island, Strait of Malacca, Malay Peninsula, Malaysia; **F,** *P. quadripartita*, Cabo Trafalgar, Spain; **G,** *P. orca*, Madang, Papua New Guinea; **H,** *P. rubrata*, Aldabra Atoll, Seychelles. All photos by T. Gosliner.

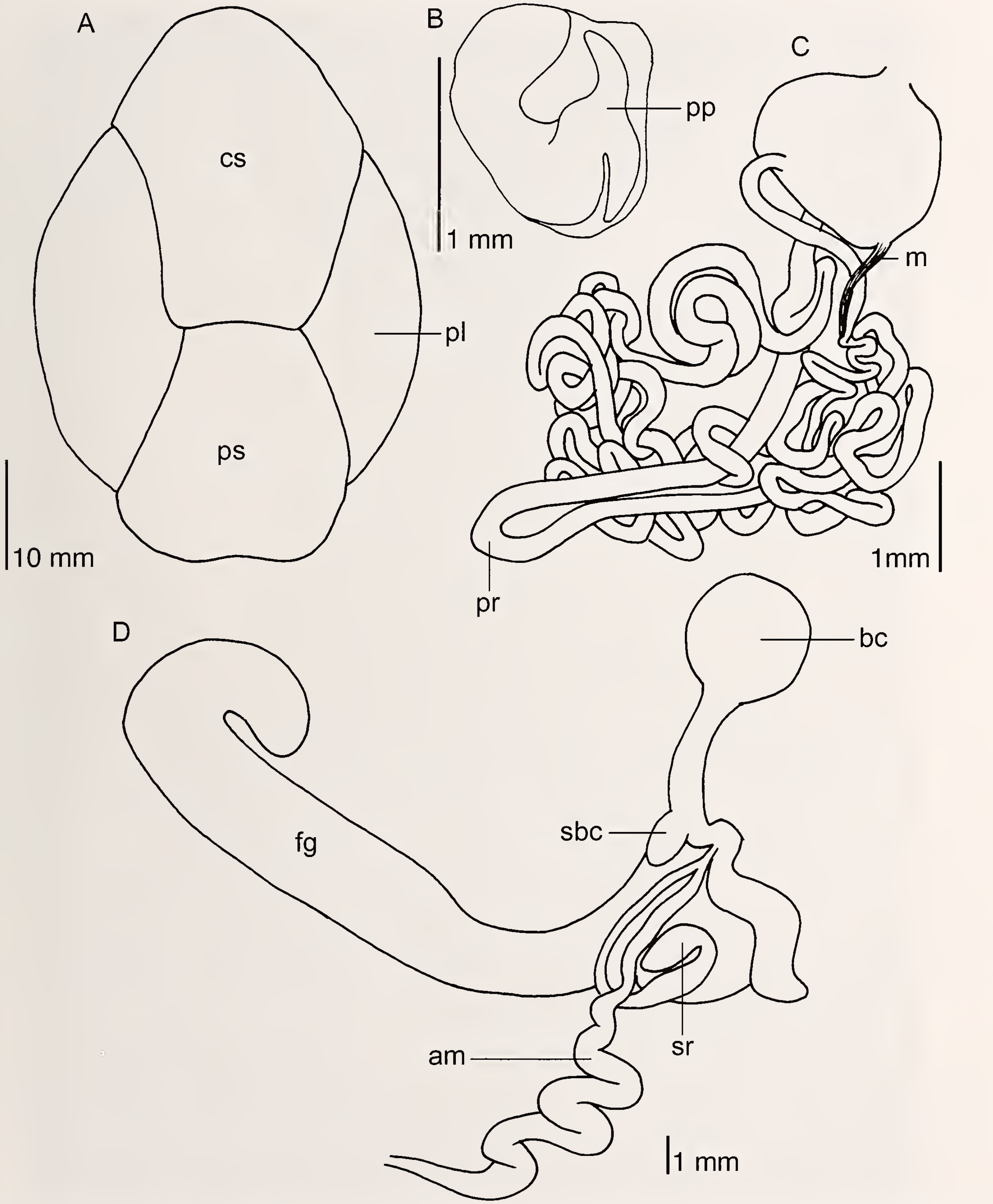

Figure 3. *Philine aperta* (SAM A54288), anatomy: **A**, dorsal view of a living animal; **B**, penis; **C**, male reproductive system; **D**, female reproductive system. Abbreviations: **am**, ampulla; **bc**, bursa copulatrix; **cs**, cephalic shield; **fg**, female glands; **m**, muscle; **pl**, parapodial lobe; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbc**, secondary bursa copulatrix; **sr**, receptaculum seminis.

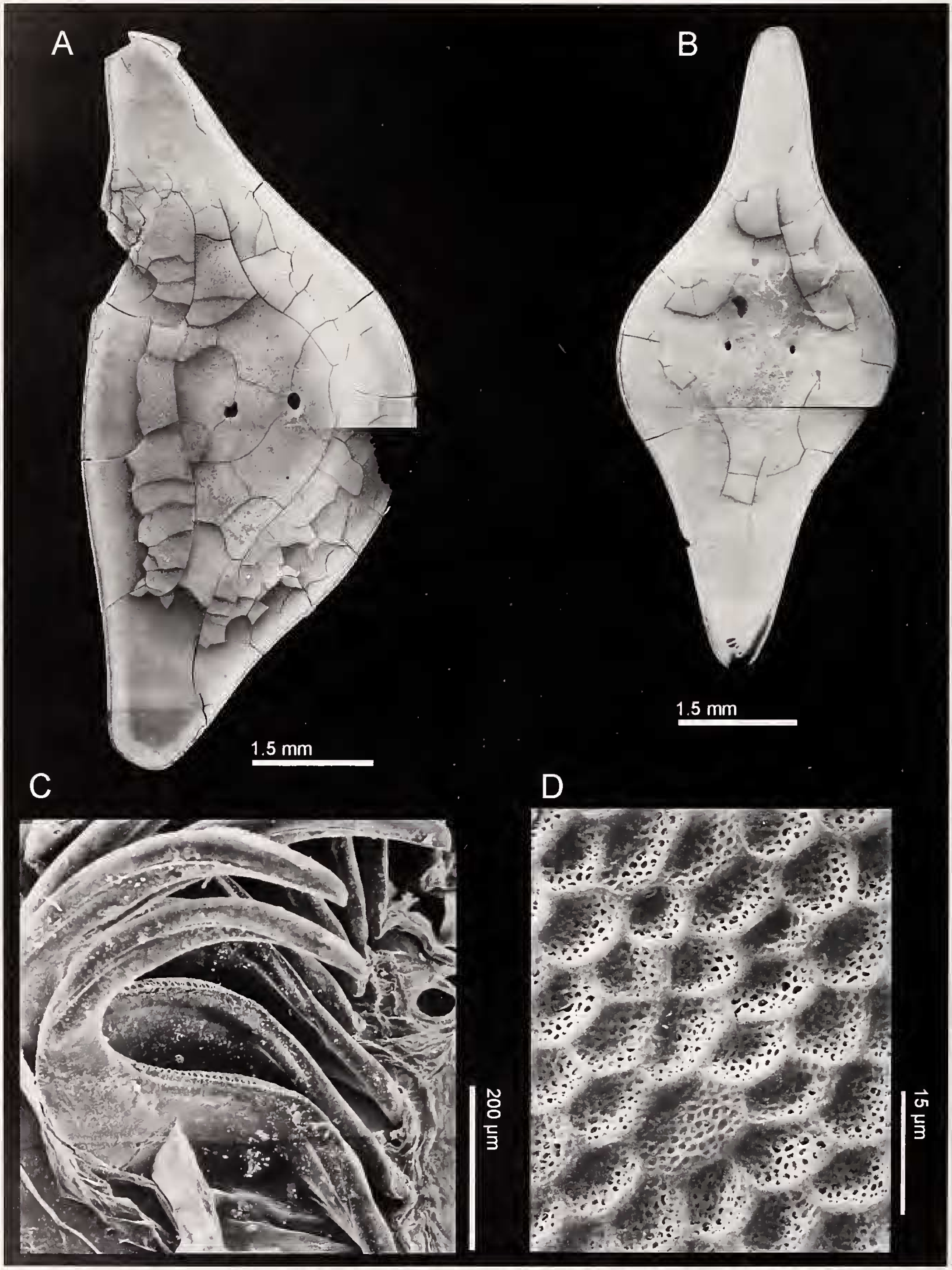

Figure 4. *Philine aperta* (SAM A54288), SEM photographs of internal hard structures: **A,** paired gizzard plate; **B,** unpaired gizzard plate; **C,** radular half-row; **D,** gizzard-plate microsculpture.

two populations by using the broader gizzard plates of *P. aperta* as the basis for separation. They called the members of the European populations *P. aperta aperta*, and they distinguished them from the members of the West African population (*P. a. guineensis*) because of their extremely wide gizzard plates. We agree with their distinction, but based on taxonomic priority, we call the European populations *P. quadripartita* and refer to the South African population *P. a. aperta sensu stricto*. The penial morphology of the Marcuses' *P. a. guineensis* is much more similar to that of *P. aperta* from southern Africa than to that of *P. quadripartita* from Europe because the penial papilla is contained within a penial sac that is not distended. It seems that the West African specimens of *P. a. guineensis* are conspecific with *P. aperta* from southern Africa, but more comprehensive study, perhaps including the addition of molecular data, is necessary to make definite conclusions.

We consider the differences between *P. aperta* and *P. quadripartita* significant at the species level. Because the type locality of *P. aperta* is South Africa, the African animals must retain the name *P. aperta* Linnaeus, 1767, and the European population should be called *P. quadripartita* Ascanius, 1772. As Bergh (1901) observed, there are differences in the penial morphology. The penial papilla of *P. quadripartita* protrudes into the base of the penial sac, which is extended over the prostate. The hammer head in *P. quadripartita* is thick, but the handle is shorter than that of *P. aperta*, and it sits at the base of the penial sac. The hammer head of *P. aperta* is at the top of the penial sac, rather than the base, and it is thin, as if it were squashed. The handle has three lobes and is somewhat convoluted; it is too long to fit neatly into the penial sac. The thin muscle that connects the prostate to the penial sac is longer in *P. quadripartita* than in *P. aperta*. The distinct penial morphology of *P. quadripartita* is also evident in figures provided by Guiart (1901) and Brown (1934:fig. 25).

In addition to the morphological differences, the two species have differently shaped egg masses. In *P. aperta* (Figure 2B), the egg mass is composed of tubular, narrow, elongate sacs that are attached to the sand by a mucous thread. In *P. quadripartita* (Guiart, 1901; Picton, 1999), the egg mass is more globular with an elongate mucous thread that is almost the same length as the globular portion. Molecular systematic studies would further clarify species boundaries and geographical isolation of populations.

Philine alba Mattox 1958

(Figures 5, 6)

Philine alba Mattox, 1958:98, pls. 33, 34.

Material: CASIZ 076681, one specimen, dissected, southern California, collected by Robert Beeman. CASIZ 101369, 15 specimens, two dissected, off Point Sur, Monterey Bay, California, 36°21.5–20.7′N, 122°0.27–0.60′W, May 10, 1994, M. Eric. Anderson on R/V *Cayuse*. CASIZ 105161, one specimen, dissected, from 445 m depth, off Darwin Island, Galápagos Islands, November 21, 1995, John E. McCosker et al., aboard *Johnson Sea Link*. LACM 63-52, two specimens dissected, more than 10 specimens still intact, 183 m, off Point Pinos, Monterey Co., California (36°38′N, 122°02′W), November 26, 1963, collected by James H. McLean. LACM 172458 two specimens, shell only, 140 m, Santa Monica Bay, California.

Distribution: The type material is from Santa Catalina Island, California (Mattox, 1958), and this species has been found from the Monterey Bay to the Gulf of California. We report the first occurrence from deep water off of the Galápagos Islands.

External morphology: The living animal is uniformly white to yellowish (Behrens & Hermosillo, 2005) with thin parapodial lobes and a long cephalic shield. The posterior shield lacks a posterior notch (Figure 5A). Individuals can reach 6 cm in length.

Internal morphology: The whorls of the shell have a high rate of expansion, and the surface lacks sculpture (Figure 6A).

This species has one short ventral oral gland and one short dorsal oral gland. The buccal mass is large (Figure 5B). The radular formula is 14–24 × 2.1.0/1.1.2 (Mattox, 1958; present study). The inner lateral teeth have zero to seven small denticles, and vestigial rachidian teeth may be present (Figure 6E). There is a distinct gizzard, although it is not muscularized. Three small, equally sized, and kidney-shaped gizzard plates rest in the bottom of the gizzard (Figure 6B, C). The gizzard plates have indistinct microsculpture (Figure 6D). The esophagus widens posteriorly. Prominent salivary glands span the esophagus from the posterior tip of the buccal mass to the anterior tip of the crop (Figure 5B).

The parietal and pleural ganglia are fused. The genital ganglion is distinct, although minute and difficult to see. Halfway between the parietal-pleural ganglion and the visceral ganglion is the supraintestinal ganglion, and the osphradial nerve branches from it (Figure 5C). The subintestinal ganglion is adjacent to the visceral ganglion.

The penial sac is large and round with a smooth sheath and two conical papillae that lack armature (Figure 5D). The simple, hook-shaped, single-lobed prostate has no convolutions.

The posterior reproductive system contains a secondary receptaculum and an unbranched hermaphro-

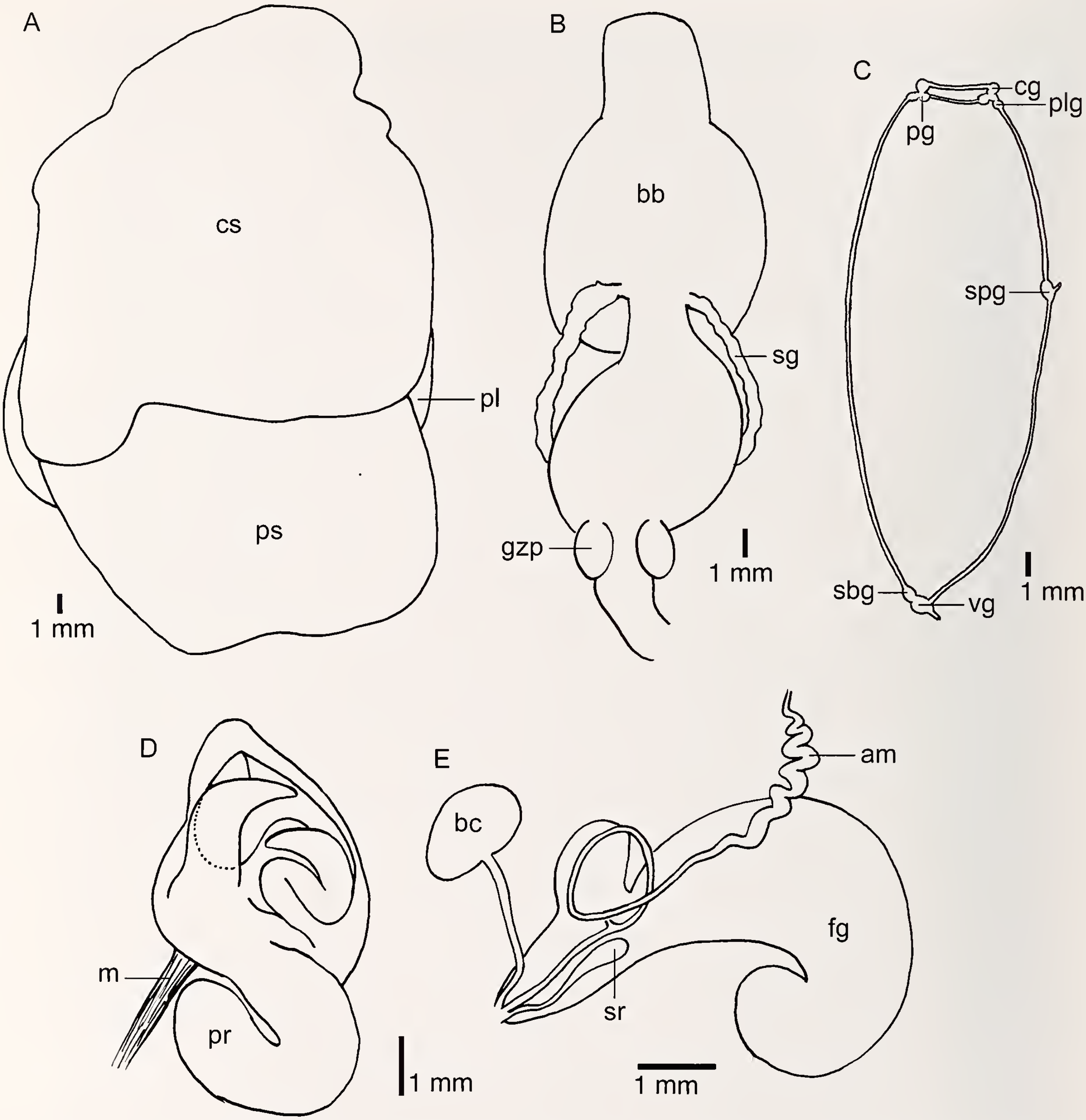

Figure 5. *Philine alba* (CASIZ 076681), anatomy: **A**, dorsal view of a living animal; **B**, anterior portion of the digestive system; **C**, nervous system; **D**, male reproductive system; **E**, female reproductive system. Abbreviations: **am**, ampulla; **bb**, buccal bulb; **bc**, bursa copulatrix; **cg**, cephalic ganglion; **cs**, cephalic shield; **fg**, female glands; **gzp**, gizzard plate; **m**, muscle; **pg**, pedal ganglion; **pl**, parapodial lobe; **plg**, parietal-pleural ganglion; **pr**, prostate; **ps**, posterior shield; **sbg**, subintestinal ganglion; **sg**, salivary gland; **spg**, supraintestinal ganglion; **sr**, receptaculum seminis; **vg**, visceral ganglion.

ditic duct (Figure 5E). The ampulla is convoluted, and there is a single receptaculum seminis located at the base of the genital aperture. The mucous gland is large and free at the distal end. There is a single bursa copulatrix.

Discussion: *Philine alba* is not part of the *P. aperta* clade (see Phylogenetic Analysis and Figures 38, 39). Our specimens closely match Mattox's original description (1958), allowing us to enhance his discussion with figures of the whole animal, radula, and gizzard

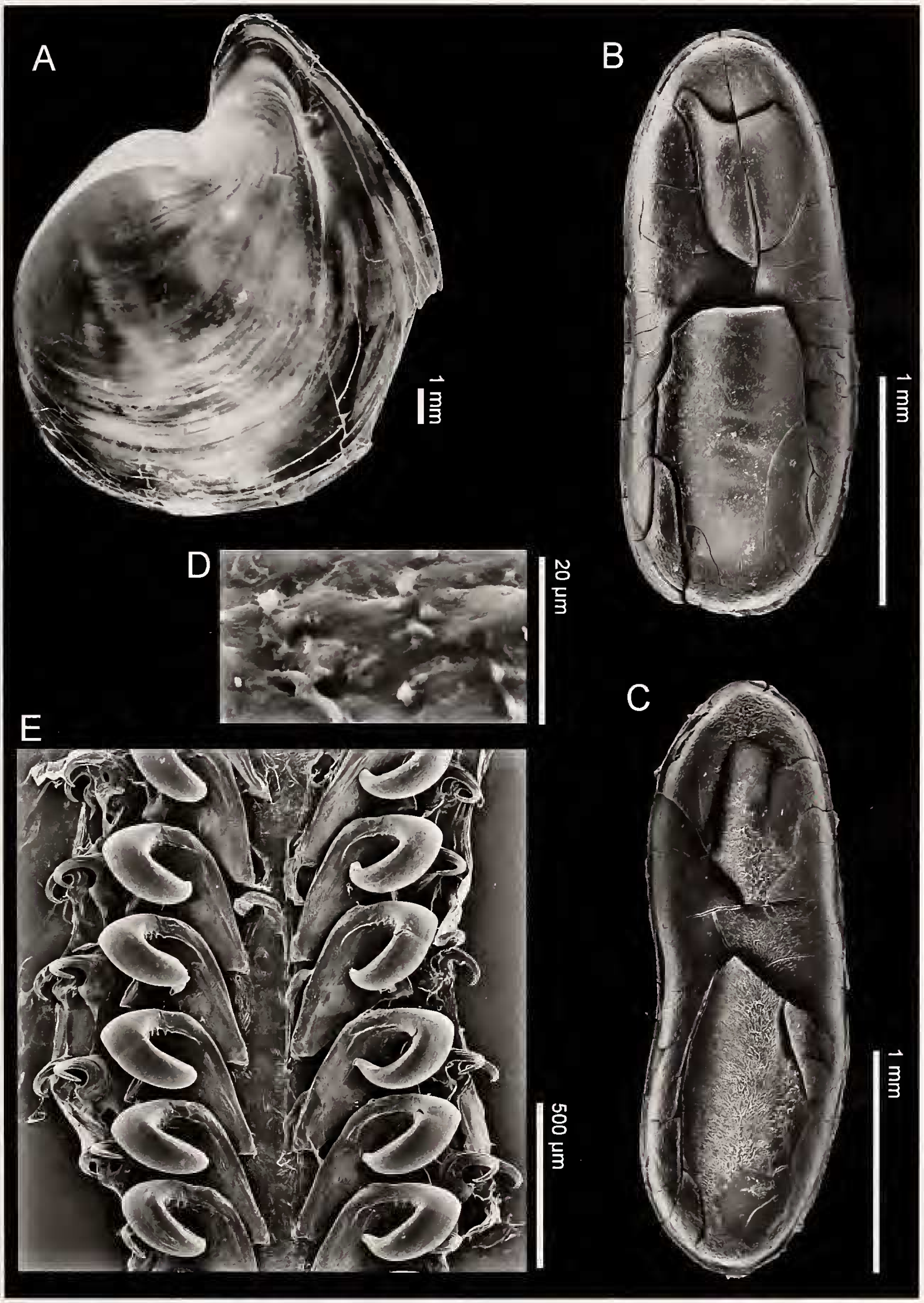

Figure 6. *Philine alba* (CASIZ 076681), micrographs of internal hard structures: **A,** light micrograph of the ventral side of the shell; **B, C,** SEM photographs of the gizzard plates; **D,** SEM photograph of the gizzard-plate microsculpture; **E,** SEM photograph of the radular teeth.

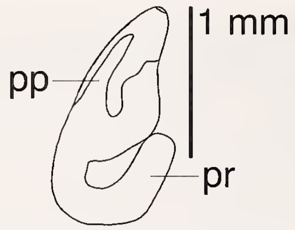

Figure 7. *Philine alboides* (USNM 897330), male reproductive system. Abbreviations: **pp,** penial papilla; **pr,** prostate.

plates. Mattox reported no rachidian teeth, but we found some that are highly reduced and probably vestigial (Figure 6E).

The specimens from California to the Galápagos Islands of the eastern Pacific differ from those that Marcus (1974) described as having a distribution from the western Atlantic of Florida to Rio de Janeiro. Marcus (1974:fig. 103) reported that the penis of her specimens had "a folded atrium and no true penial papilla," but our specimens (Figure 5D) and Mattox's had multilobed papillae (Mattox, 1958). Furthermore, the gizzard plates in Mattox's specimens are small ovals with a convex inner surface, whereas in Marcus's specimens they are pointed on the inner surface, reminiscent of the gizzard plates of members of the genus *Scaphander*. In all likelihood, Marcus's specimens represent a distinct species. Additional material from the Atlantic is compared to confirm these apparent distinctions, but the two seem to be distinct species from different ocean basins.

Philine alboides Price, Gosliner, and Valdés, sp. nov.

(Figures 7, 8)

Philine alba Mattox, 1958; Marcus and Marcus, 1967:607, figs. 23–28; Marcus, 1974:359, figs. 102, 103, misidentification.

Material: Holotype: USNM 836707, Station 199, R/V *Pillsbury*, 311–329 m depth, off the east coast of Florida, between 27°59′N, 79°20′W and 27°30′N, 79°10′W, August 11, 1964. Paratypes: USNM 897330, one specimen, 329 m depth, off Louisiana, Gulf of Mexico, 28°04′N, 90°17′W, November 6, 1963, R/V *Gyre*. USNM 836704, R/V *Pillsbury*, Station 446, one specimen, dissected, 110–298 m depth, Gulf of Mosquitos, Panama, 8°580′6″N, 81°26′18″W, July 21, 1966.

Distribution: Known from the Straits of Florida, the Gulf of Mexico (Louisiana; present study) and the Caribbean to Rio de Janeiro, Brazil (Marcus & Marcus, 1967; Marcus, 1974).

Etymology: The name *alboides* is a noun in apposition and comes from the Latin meaning 'like alba.' It refers to the fact that this species has previously been confused with *P. alba*. Type locality: Straits of Florida, USA.

External morphology: The preserved animal is uniformly white, 19–44 mm in length with thin parapodial lobes and a long cephalic shield. The posterior shield lacks a posterior notch.

Internal morphology: The whorls of the shell have a high rate of expansion, and the surface lacks sculpture. Because the shell is fragmented, we left it in the animal and could not take a scanning electron image. Its shape is open and broad as in *P. alba*.

This species has one short ventral oral gland and one short dorsal oral gland. The buccal mass is large. The radular formula is 16 × 2.1.0.1.2 in the holotype. The inner lateral teeth lack any trace of denticles, and vestigial rachidian teeth are absent (Figure 8A). There is a distinct gizzard, although it is not muscularized. Only one gizzard plate (Figure 8B) was found in the partially dissected holotype specimen, but all three plates were contained in a vial in one paratype (USNM 836704). The plates are ovoid at the base and sharply angled with a high, rounded apex. The esophagus widens posteriorly. Prominent salivary glands span the esophagus from the posterior tip of the buccal mass to the anterior tip of the crop.

The parietal and pleural ganglia are fused. The subintestinal ganglia and visceral ganglia are adjacent to each other; a distinct genital ganglion was not evident and is presumably fused to the visceral ganglion. Halfway between the parietal-pleural ganglion and the visceral ganglion is the supraintestinal ganglion, and the osphradial nerve branches from it. The penial sac is large and round with a smooth, conical papilla that lacks armor (Figure 7). The relatively short prostate curves anteriorly. The posterior reproductive organs were examined in one paratype (USNM 836704).

The ampulla is highly convoluted, and it curves around the smaller albumen and membrane glands. A proximal receptaculum was not evident but that may be because the specimen was not particularly well preserved. The hermaphroditic duct branches to the albumen and membrane glands and continues as an elongate tube. Immediately before its junction with the genital aperture, it is joined by a distal receptaculum seminis. The duct of the large, rounded bursa copulatrix is moderately long and joins the bulbous genital atrium, where a single bursa copulatrix also is situated.

Discussion: Although *P. alboides* is not part of the *P. aperta* clade (see Phylogenetic Analysis), we recognized

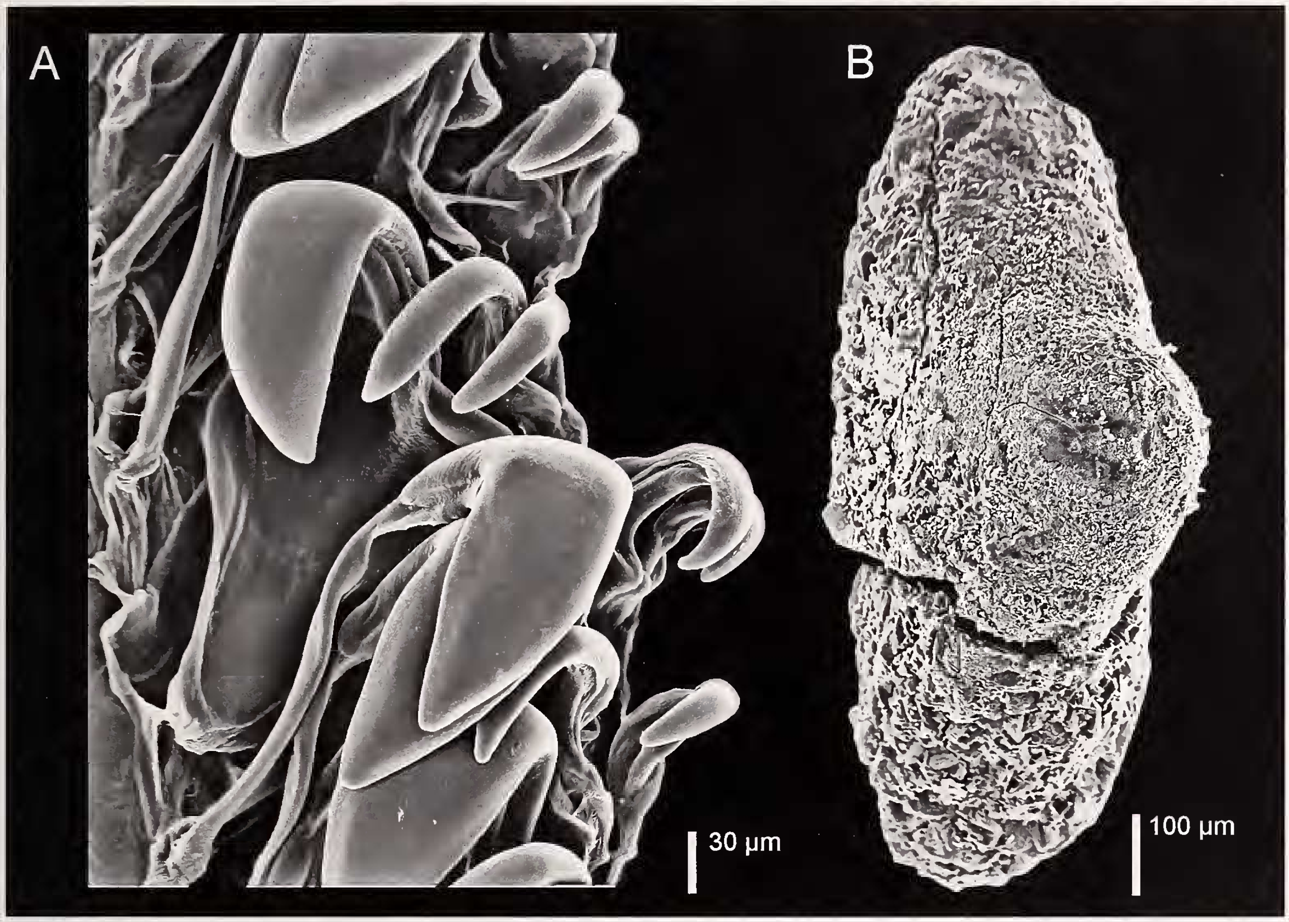

Figure 8. *Philine alboides* (USNM 897330), SEM photographs of internal hard structures: **A,** Radular teeth; **B,** gizzard plate.

the distinction between this species and *P. alba* while undertaking this study.

Our specimens closely match the descriptions in Marcus & Marcus (1967) and Marcus (1974) of *P. alba*, and their illustrations are, with the exception of the anatomy of the penial papilla (illustrated herein in Figure 7), sufficient for identifying this species. The present material and the Marcuses' descriptions have several consistent morphological differences with that of *P. alba*, which is known only from the eastern Pacific. *Philine alboides* has a radula with inner lateral teeth lacking denticles, whereas *P. alba* always has small denticles. The gizzard plates of *P. alboides* are more rounded and higher in profile than the ovoid, more flattened plates of *P. alba*. The penis of *P. alboides* has a recurved simple prostate whose distal end faces anteriorly (Marcus & Marcus, 1967; Marcus, 1974; present study), whereas that of *P. alba* is directed posteriorly. In addition, the penial papilla of *P. alboides* has a single primary papilla, whereas in *P. alba* two distinct papillae are present. Based on the consistency of these differences and the fact that the two taxa are separated by the Isthmus of Panama, we consider the Atlantic material to represent a distinct species, which we call *P. alboides*. Both *P. alba* and *P. alboides* are unique among described *Philine* species in a having a distal receptaculum seminis situated near the genital atrium.

Philine angasi (Crosse & Fischer, 1865)

(Figures 9, 10)

Bullaea angasi Crosse and Fischer, 1865:38, pl. 2.
Philine angasi (Crosse and Fisher), Rudman, 1970:30, figs. 1A, F–H, pl. 3G; Rudman, 1972b:460, figs. 1–4.

Material: BMNH 1996408, 12 specimens (3 dissected), Port Jackson, Sydney, New South Wales, Australia, collected by I. Bennett.

Distribution: Known from northern New Zealand and from southern Australia in portions of New South Wales, Victoria, Tasmania, South Australia, and southern Western Australia (Rudman, 1970).

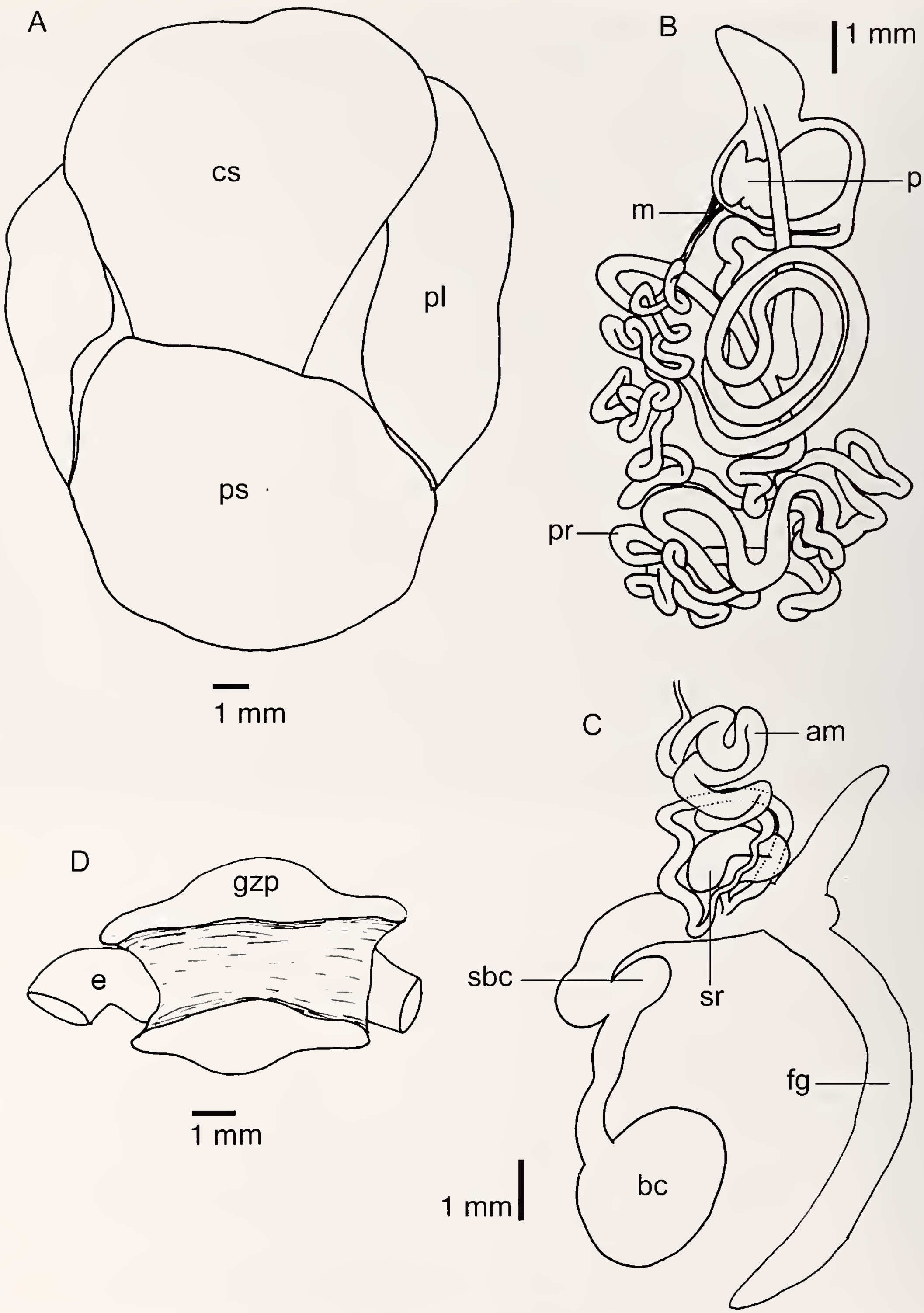

Figure 9. *Philine angasi* (BMNH 1996408), anatomy: **A,** dorsal view of a living animal; **B,** male reproductive system; **C,** female reproductive system; **D,** gizzard. Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **cs,** cephalic shield; **e,** esophagus; **fg,** female glands; **gzp,** gizzard plate; **m,** muscle; **pl,** parapodial lobe; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbc,** secondary bursa copulatrix; **sr,** receptaculum seminis.

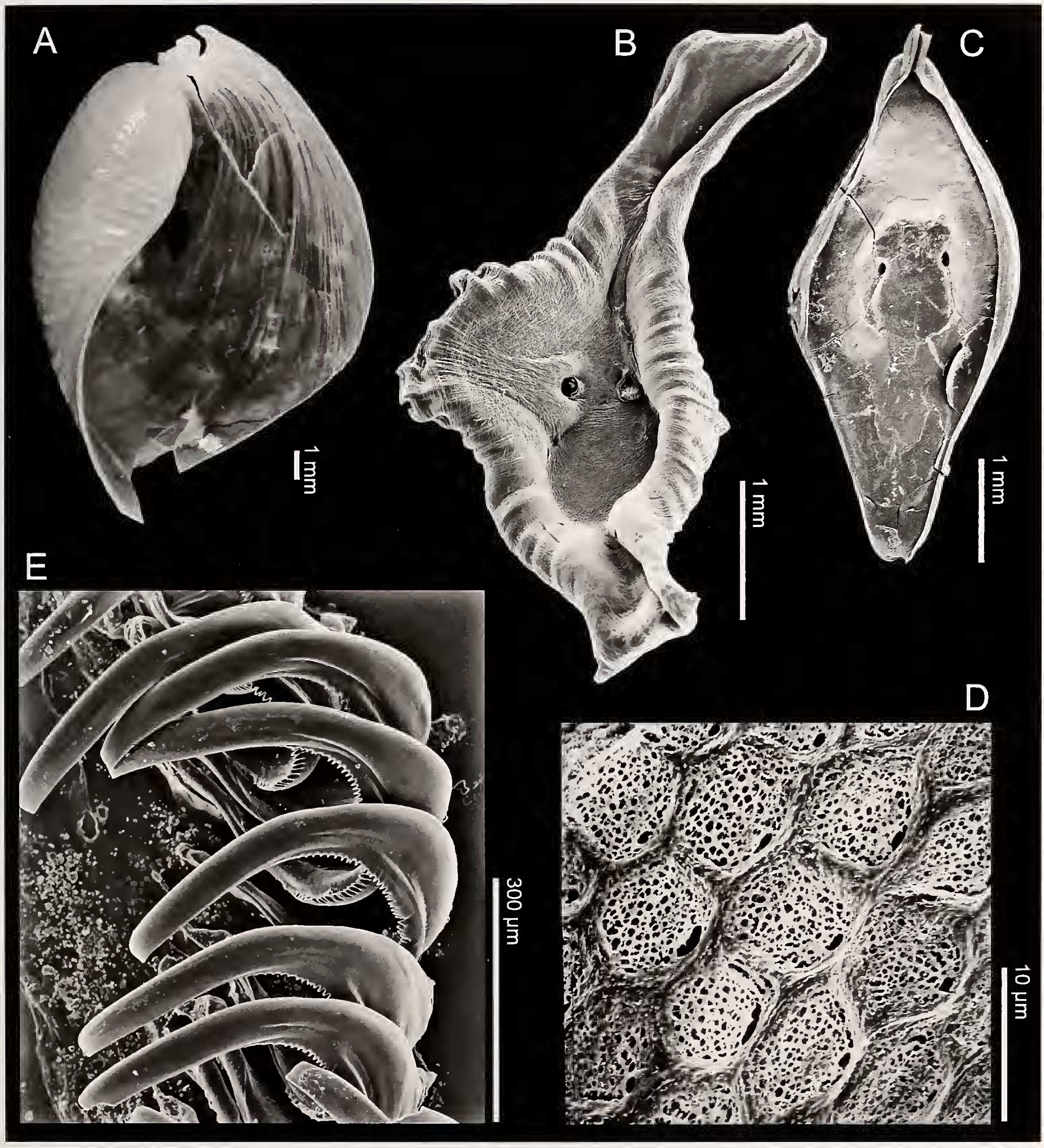

Figure 10. *Philine angasi* (BMNH 1996408), micrographs of internal hard structures: **A,** light micrograph of the ventral side of the shell; **B,** SEM photograph of a paired gizzard plate; **C,** SEM photograph of the unpaired gizzard plate; **D,** SEM photograph of the gizzard-plate microsculpture; **E,** SEM photograph of the radular teeth.

External morphology: The preserved animals are uniformly white (Rudman, 1998b) and reach 10 cm in length. The cephalic shield is longer than the posterior shield, and the parapodial lobes are thin (Figure 9A). The posterior shield does not have a notch in the preserved specimens, but the photograph of the living animal (Rudman, 1998b) clearly shows a well-developed notch.

Internal morphology: The shell is relatively tightly coiled for this clade (Figure 10A), and it has a spine on the last whorl where the outer lip meets the spire. The surface lacks punctation but is slightly ribbed.

There are two ventral oral glands, but this species lacks dorsal oral glands. The radular formula is 20 × 1.0.1. The broad inner lateral teeth have approximately 50–60 small denticles (Figure 10E). The gizzard is muscularized and surrounded by large gizzard plates (Figure 9D); it lacks a distinct crop posterior to the plates. The three spindle-shaped plates have medium-sized pores (Figure 10B, C) and a microsculpture that consists of regularly arranged polygons (Figure 10D). One plate (Figure 10C) is smaller than the two paired plates (e.g., Figure 10B). The salivary glands are short.

The supraintestinal ganglion is located toward the anterior of the visceral loop and is adjacent to or adjoining the fused pleural-parietal ganglion. The subintestinal ganglion is adjacent to the visceral ganglion, but the genital ganglion remains distinct.

The penial papilla is hammer-shaped with subequal lobes and sits directly on a cushion-shaped base that does not distend the wide penial sac (Figure 9B). The convoluted prostate branches to a long, coiled ejaculatory duct that is surrounded by the prostate. A short muscle connects the end of the prostate to the sac.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figure 9C). The mucous gland is large, and it bends at the free end. There is a single secondary bursa copulatrix.

Discussion: *Philine angasi* is the only species in the *P. aperta* clade that has a spine on the spire side of the last whorl of the shell. The spine is short and stubby.

The paired gizzard plates are similar to those of *P. elegans*, in that they have an S-like twist to their shape. The edges lack the fringes found in *P. elegans*, but they are crenulated. The unpaired plate is symmetrical and more oblong than the homologous plate in *P. elegans*. The microstructure of the gizzard plate consists of a mesh of regularly shaped polygons, as in *P. aperta* and *P. puka*.

The penial morphology of *P. angasi* is most similar to that of *P. orientalis*. These papillae are relatively small and columnar, although *P. angasi* lacks an additional lobe on the base of the papilla that is present in *P. orientalis*.

Philine auriformis Suter, 1909

(Figures 2C, 11, 12)

Philine auriformis Suter, 1909:157. Rudman, 1970: 24, fig. 1b–e, 2P, pl. 3, figs. d–f, h, o; Gosliner, 1995:122, figs. 1–3.

Material: CASIZ 097499, approximately 100 specimens, 10–35 mm preserved length, three dissected, trawled in 4 m depth, between Dumbarton and San Mateo Bridges on western side of San Francisco Bay, California, July 30, 1993, T. Gosliner et al.

Distribution: *Philine auriformis* is originally from New Zealand (Rudman, 1970, 1972a, b). It has been introduced to the western coast of North America and can now be found from San Diego to Bodega Bay (Gosliner, 1995).

External morphology: The living animal (Figure 2C) is uniformly white, varying in length from 1 to 4 cm. The broad cephalic shield is longer than the posterior shield (Figure 11A). The posterior shield is notched, and the parapodial lobes are flimsy.

Internal morphology: The whorls of the shell have a high rate of expansion, and the perimeter of the shell is ovate (Figure 12). The sculpture is punctate.

There is a single, short ventral oral gland and two dorsal oral glands. The radula has the formula 21 × 1.1.0.1.1. The broad inner lateral teeth have 30 to 50 denticles. The crop is indistinct, and the gizzard is muscularized. The gizzard plates, however, are not covered with muscles, and the esophagus passes between them. The three spindle-shaped plates have approximately the same size and shape. Each plate has two long indentations on the dorsal side.

The fused pleural-parietal ganglion is adjacent to or adjoining the anterior supraintestinal ganglion. The osphradial nerve may branch from the supraintestinal ganglion or from halfway between the supraintestinal and visceral ganglia. The genital ganglion is fused to the visceral ganglion and is adjacent to the subintestinal ganglion.

The small penial papilla is hammer-shaped (Figure 11C). The penial sac is pyriform (Figure 11B). The lobes of the hammer head are subequal, the smaller of which looks like a little knob above the papilla stalk. The convoluted prostate branches, and a short muscle connects it to the end of the penial sac. The ejaculatory duct is short and completely surrounded by the convoluted prostate.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis. The large mucous gland has two lobes, and the free end bends over. There is a knob at the wide base of the spherical, thin-walled bursa copulatrix.

Discussion: Gosliner (1995) observed that this species, originally described from New Zealand, was introduced to the California coast. Rudman (1998a) disagreed with the identification, claiming that the ejaculatory duct in the California specimens was much smaller than specimens from New Zealand and that the size of the

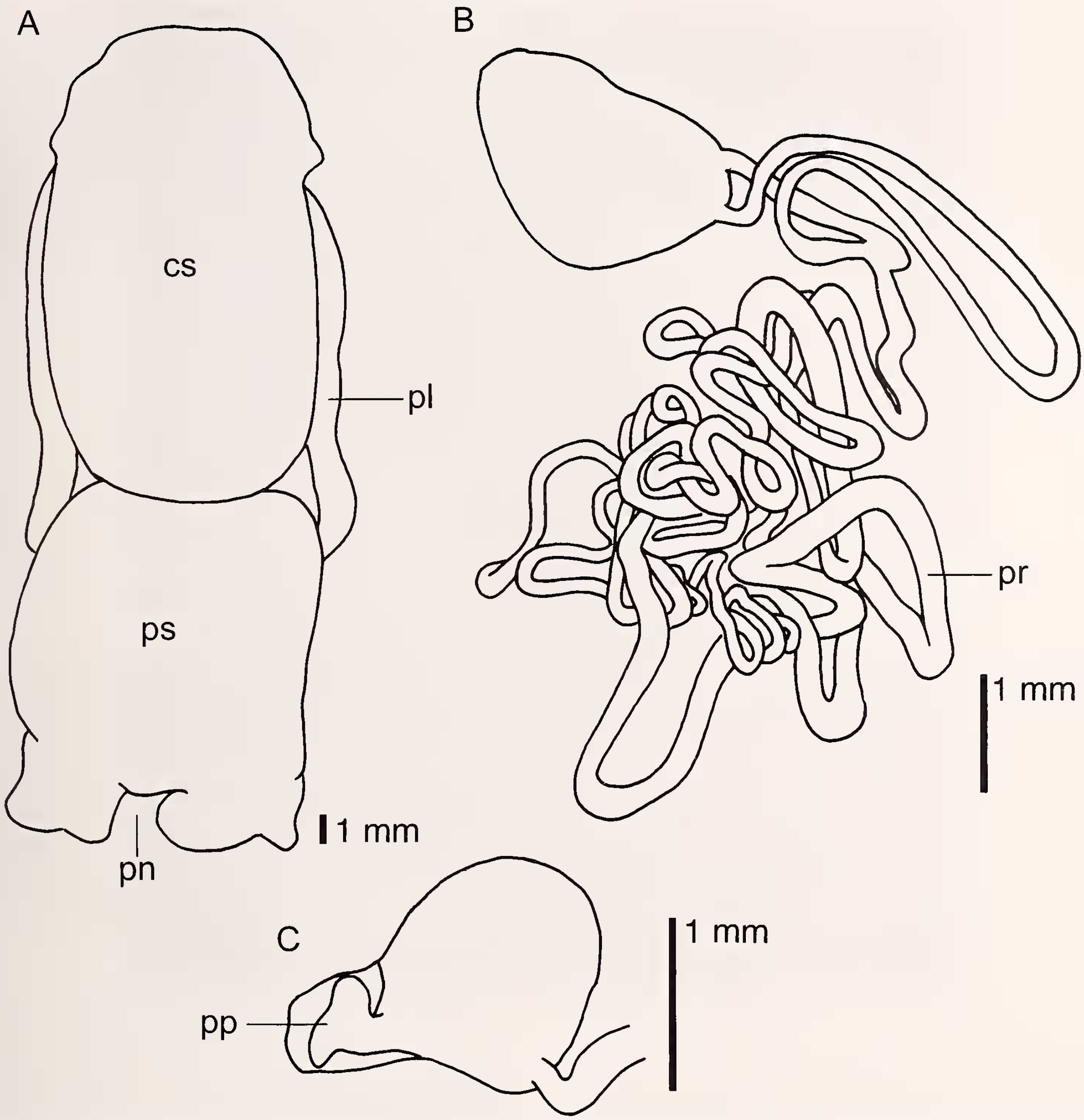

Figure 11. *Philine auriformis* (CASIZ 097499), anatomy: **A**, dorsal view of a living animal; **B**, male reproductive system; **C**, penis. Abbreviations: **cs**, cephalic shield; **pl**, parapodial lobe; **pn**, posterior notch; **pp**, penial papilla; pr, prostate; **ps**, posterior shield.

entire radula differed and was much smaller in the New Zealand specimens. However, Rudman illustrates considerable variation in the degree of elaboration of the ejaculatory duct on his website. The ejaculatory duct illustrated in Gosliner's article is intermediate between the extremes that Rudman illustrates from New Zealand and California. The specimen from California illustrated here (Figures 11, 12) is much more similar to Rudman's specimen from New Zealand than it is to the specimen he illustrated from California. Given this variation, there is no reason to suggest that these represent different species, especially because *P. auriformis* is the only large species with this type of distinctive gizzard-plate morphology. The only other species with similar gizzard plates is *Philine fenestra*, described here. Also, *P. auriformis* is the only species found near shallow-water harbors that would probably be introduced through ballast water discharge (Gosliner, 1995).

The three equal-sized gizzard plates and the punctate shell suggest this species is plesiomorphic in the *P. aperta* clade. *Philine fenestra*, *Philine finmarchica*, and

Figure 12. *Philine auriformis* (CASIZ 097500). Light micrograph of the ventral side of the shell.

Philine thurmanni thurmanni are the only other members of this clade that have equal-sized plates. The penial papilla of *P. auriformis* is hammer-shaped, although the hammer is much smaller than in other members of the clade; the lobes barely protrude over the base of the papilla. The slits on the gizzard plates are shallower and shorter than those found on the plates of *P. fenestra*. The shell and posterior reproductive system has been illustrated previously (Gosliner, 1995), although we have provided additional detail regarding the penial morphology.

Philine babai Valdés, 2008

(Figure 13)

Philine babai Valdés, 2008:721–722, figs. 64C–E, 67.

Material: MNHN (no specimen number), one dissected specimen, Station DW08, 435 m, New Caledonia, 20°134′S, 164°54′W.

Distribution: *Philine babai* is known from Indonesia, Fiji, New Caledonia, Tonga, and Wallis Island from 230 to 533 m.

External morphology: The preserved animals are uniformly white and approximately 2 cm in length. The cephalic shield is longer than the posterior shield. The posterior shield lacks a posterior notch. The parapodial lobes are narrow.

Internal morphology: The whorls of the shell are tightly coiled for this clade, and the shell is punctate.

There are no ventral or dorsal oral glands. The

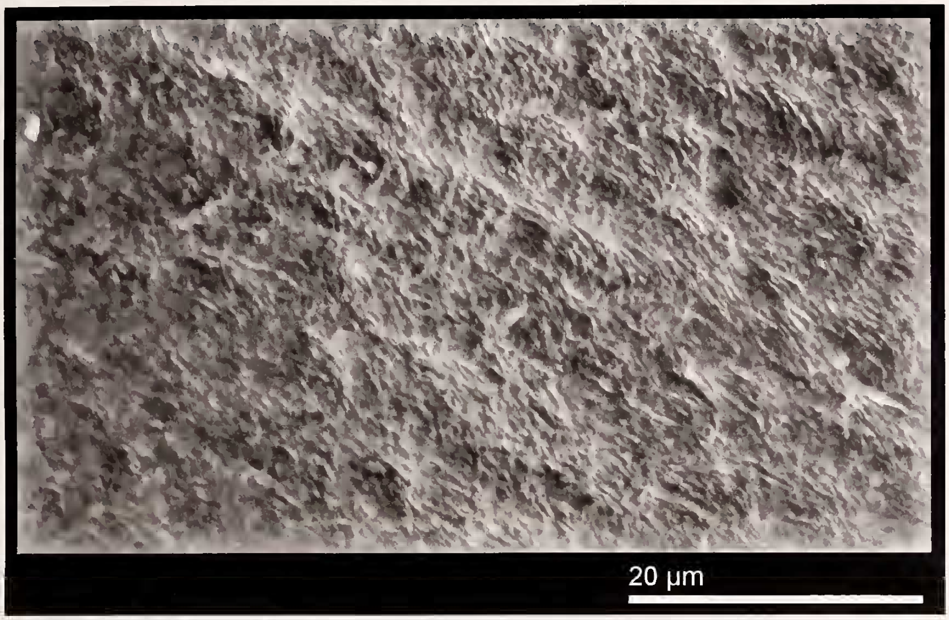

Figure 13. SEM photograph of the gizzard-plate microsculpture of *P. babai* (MNHN no specimen number).

buccal bulb is small, and the radular formula is 16 × 1.0.1 with 35 small denticles on the inner side of the broad inner lateral teeth. The crop is indistinct. The gizzard is muscularized, but the three plates are not covered with muscles. The plates are roughly spindle-shaped. The central plate is broad with a ruffled edge, smaller than the other two, and has two small slits, one on each edge of the outer side of the plate. The paired plates are mirror images of each other, and they have an S-like twist, and two long slits on the sides. The slit on the inner edge is longer than the slit on the outer edge. The microsculpture of the gizzard plates lacks structure (Figure 13). The salivary glands are short.

The fused pleural-parietal ganglion adjoins the anterior supraintestinal ganglion. The osphradial nerve branches may branch from the supraintestinal ganglion or from halfway between the supraintestinal and visceral ganglia. The genital ganglion remains distinct from the visceral ganglion but is fused to the subintestinal ganglion.

The hammer-shaped penial papilla has subequal lobes and distends the base of the pyriform penial sac over the convoluted prostate. The papilla rests directly on the base of the penis, and is not supported by a stalk. The ejaculatory duct branches from the convoluted prostate, and a short muscle connects the end of the prostate to the sac. The ejaculatory duct is long.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches a single, long, and narrow receptaculum seminis (Figure 14). The female gland is relatively small for this clade. The bursa copulatrix is large with a single secondary bursa copulatrix.

Discussion: *Philine babai* (Valdés, 2008), *P. auriformis*, *P. fenestra*, *Philine infundibulum*, and *Philine sarcophaga* all have slits on their gizzard plates, although *P. sarcophaga* and *P. infundibulum* lack slits on their unpaired plates. The plates of *P. auriformis* and *P. fenestra* are all the same size and shape, which makes *P. babai* the only species with slits also present on its wide, unpaired plate. The slits on the unpaired plate of *P. babai* however are very reduced. This unpaired plate has ruffled edges; these ruffles are much broader than the crenulations edging the paired plates in *P. angasi*. The unpaired plate is rhomboidal, as are the unpaired plate of *P. elegans*, *P. infundibulum*, and *P. sarcophaga*. The gizzard plates lack any discernible microsculpture.

The reduced penial papilla in *P. babai* (Valdés, 2008) is similar to that in *P. auriformis*. The tip of the papilla has slightly unequal lobes, and the papilla rests on a fat base.

Philine elegans Bergh, 1905

(Figure 2D, 15, 16)

Philine elegans Bergh, 1905:31, pl. 9, figs. 9–13.

Material: CASIZ 083758, one specimen, dissected, Anilao, Mabini, west side of Calumpan Peninsula, Batangas Province, Luzon Island, Philippines, collected February 23, 1992 by T. M. Gosliner. California

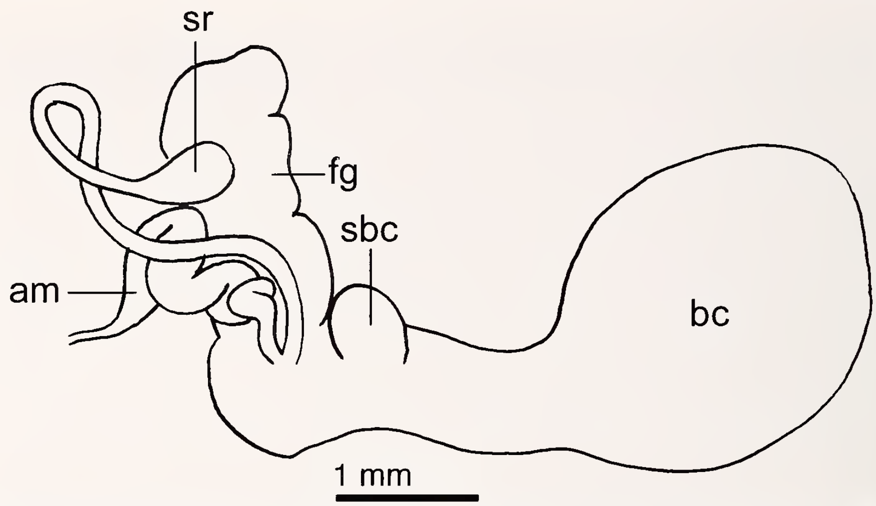

Figure 14. Female reproductive organs of *P. babai* (MNHN no specimen number). Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **fg,** female glands; **sbc,** secondary bursa copulatrix; **sr,** receptaculum seminis.

Academy of Sciences, San Francisco, CASIZ 086710, two specimens, one partially dissected, Wair Mitak, Flores, Indonesia, collected April 25, 1992 by P. Fiene.

Distribution: Specimens have been found from Saleh Bay, Subawa Island (type locality), and Flores Island, Indonesia (Bergh, 1905; present study) and Luzon Island, Philippines (present study).

External morphology: The living animal (Figure 2D) is uniformly white and approximately 1 cm in length. The cephalic shield is longer than the posterior shield (Figure 15A). The parapodial lobes are thin, and the posterior notch is deep.

Internal morphology: The shell was not preserved in the material we studied, so we concluded from an apical drawing in Bergh (1905) that the whorls of the shell have a high rate of expansion. The surface of the shell is smooth.

There are two short, closely appressed dorsal oral glands and one short ventral oral gland. The buccal bulb (Figure 15B) and radula are reduced; the radular formula is 21 × 1.0.1. The inner lateral tooth is broad with 33 denticles on the oldest tooth and 51 on the youngest (Figure 16D). The crop is indistinct. The gizzard is muscularized, but the large plates are not covered with muscles. The gizzard plates are delicately fringed around the margin (Figure 16A, B). The fringes are irregularly spaced around the margin of the plate. The unpaired plate is small and either diamond-shaped or oval (Figure 16A). The other two plates are approximately the same size and shape. These two plates are roughly spindle-shaped with an S-like twist (Figure 16B). All three plates have pores. The micro-sculpture is made of deep, regular impressions that are larger than the impressions found in other species (Figure 16C). The salivary glands are short.

The fused pleural-parietal ganglion is adjacent to the anterior supraintestinal ganglion (Figure 15B). The osphradial nerve branches from the right lateral nerve midway between the supraintestinal and visceral ganglia. The genital ganglion is fused to the visceral ganglion and is adjacent to the subintestinal ganglion.

The penial sac is ovate (Figure 15C). The base of the penial papilla is a round cushion. A short stalk leads up to the hammer-shaped penial papilla. The basal lobe of the hammer is much shorter than the other lobe. The convoluted prostate branches to a short ejaculatory duct that is completely surrounded by the convoluted prostate.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figure 15D). The large mucous gland bends at its free end. There is a single secondary bursa copulatrix.

Discussion: This record of *P. elegans* is the first since Bergh's original description (Bergh, 1905), which was based on one specimen. The type material seems to be lost: it is not present in the collections of the Zoologisk Museum, Copenhagen, where most of Bergh's remaining types are housed. Bergh described much of the anatomy of this species and illustrated the early whorls of the shell, the fringed gizzard plates, and a radular tooth. The species is autapomorphic for fringed gizzard plates, and is therefore easy to recognize. The large paired plates are most similar to those found in *P. angasi*, but the extensions are much larger, and the paired holes are close to each other. They are a modified version of the tricornered hat found in *P. aperta*, because the plates are slightly twisted along the

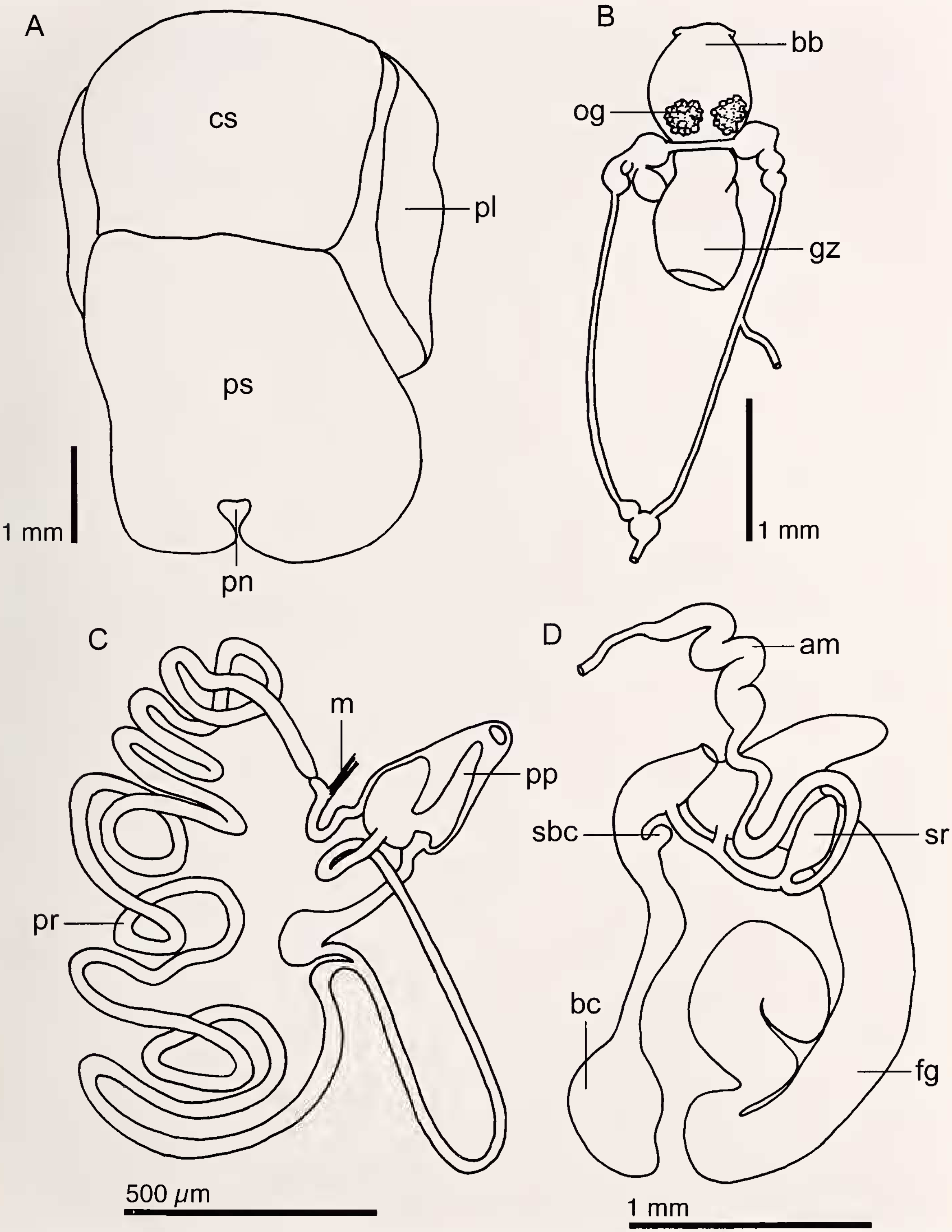

Figure 15. *Philine elegans* (CASIZ 083758). Anatomy. **A,** dorsal view of a living animal; **B,** anterior portion of the digestive system and nervous system; **C,** male reproductive system; **D,** female reproductive system. Abbreviations: **am,** ampulla; **bb,** buccal bulb; **bc,** bursa copulatrix; **cs,** cephalic shield; **fg,** female glands; **gz,** gizzard; **m,** muscle; **og,** oral gland; **pl,** parapodial lobe; **pn,** posterior notch; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbc,** secondary bursa copulatrix; **sr,** receptaculum seminis.

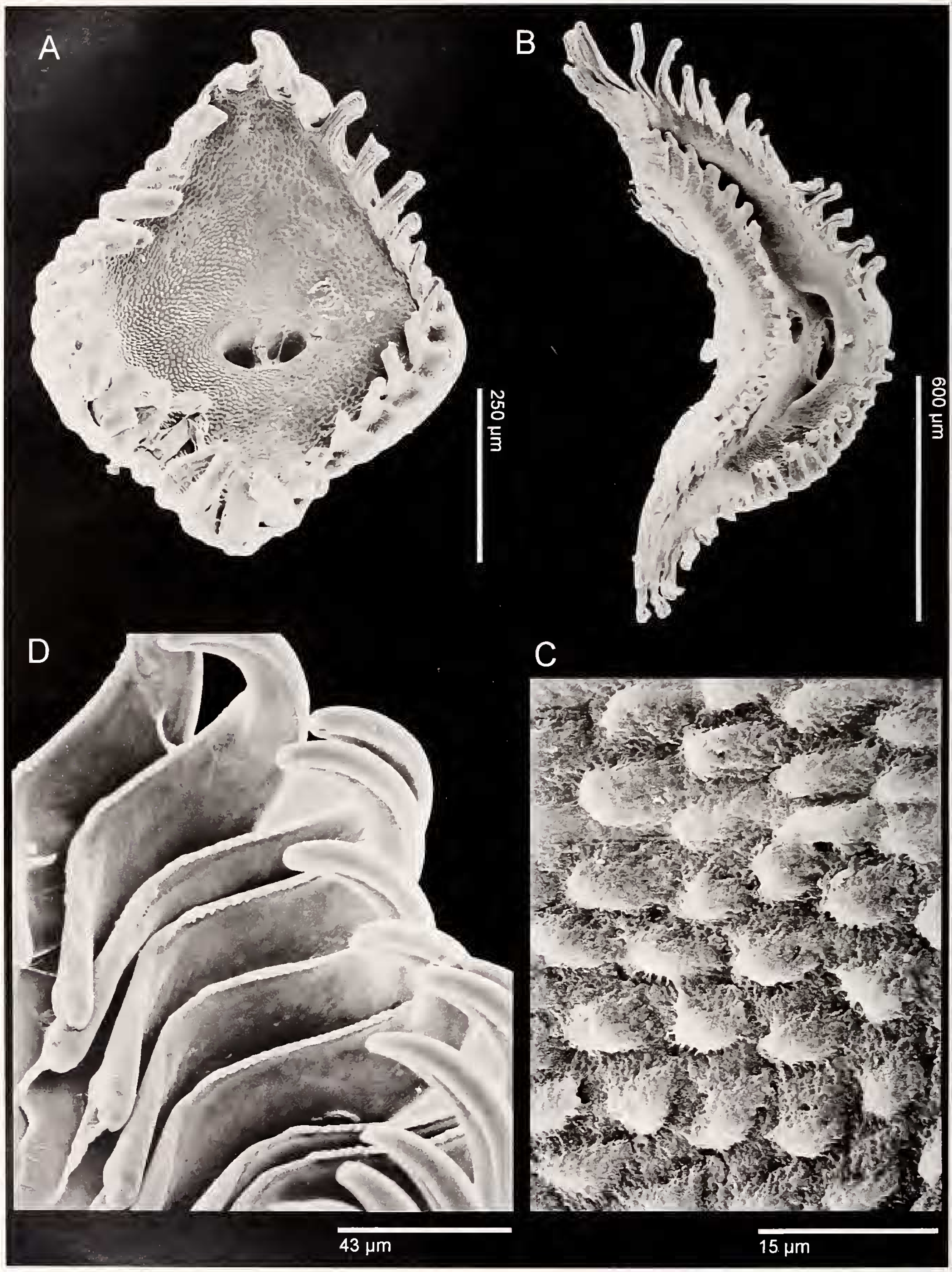

Figure 16. *Philine elegans* (CASIZ 083758), SEM photographs of internal hard structures: **A,** paired gizzard plate; **B,** unpaired gizzard plate; **C,** radular teeth; **D,** gizzard-plate microsculpture.

long axis. The smaller, unpaired plate is diamond-shaped, similar to that in *Philine habei* (Valdés, 2008), but with paired holes that are situated close to each other. The microsculpture of the plates is much smaller than in other species, although it is easier to see because of the deep, regular indentations.

The hammer head of the penial papilla has markedly unequal lobes, as in *P. puka*. The base of the papilla is round and lacks lobes.

The specimens were in Bouin's solution, which dissolved the shell. We based our assessment of the shell characters on Bergh's (1905) drawings.

Philine fenestra Price, Gosliner, and Valdés, sp. nov.

(Figures 17, 18)

Type material: Holotype: SAM, University of Cape Town Ecological Survey, Station SCD 129C, specimen 4–5 mm, coarse sand, 100 m depth, 34°48′S, 22°06′E, June 3, 1960. Paratypes: SAM, University of Cape Town Ecological Survey, Station FB 402A, False Bay, South Africa, three specimens, 4–6 mm, one dissected, fine sand, 31 m depth, 34°8.8′S, 18°33.5′E, May 16, 1961. University of Cape Town Ecological Survey, Station SCD 334 T-V, one specimen 3 mm, mud, 42 m depth, 34°02′S, 23°27′E, February 11, 1962. University of Cape Town Ecological Survey, Station SCD 129C, specimen 4–5 mm, coarse sand, 100 m depth, 34°48′S, 22°06′E, June 3, 1960. CASIZ 175004, one specimen, University of Cape Town Ecological Survey, Station SCD 186M, specimen 18 mm, mud, 97 m depth, 34°10′S, 23°32′E, November 30, 1960. CASIZ 175003, University of Cape Town Ecological Survey, Station NAD, two specimens 12–23 mm, one dissected, sand and mud, 175–200 m depth, 32°E, 29°37.5′S, 31°33′E, September 8, 1960.

Distribution: This species is known only from South Africa, where it has been found from False Bay to northern Kwazulu Natal.

Etymology: The name *fenestra*, a noun in apposition, is Latin for window and refers to the slits on the gizzard plates that are covered by a clear, hard (window-like) layer.

Type locality: False Bay, South Africa.

External morphology: The preserved animals are 3–12 mm in length. They are uniformly white with a long cephalic shield, and the posterior shield lacks a notch on its posterior end (Figure 17A). The parapodial lobes are narrow and not muscular.

Internal morphology: The whorls of the shell are tightly coiled for this clade (Figure 18A). The shell surface is punctate throughout (Figure 18B).

There are two dorsal oral glands and one ventral oral gland. The radular formula is 18 × 1.1.0.1.1. The inner lateral teeth have a broad lateral ridge that is covered by 35–50 small denticles, and the outer lateral teeth are small, narrow, and elongate (Figure 18F). The gizzard is muscularized, but the three large plates are not covered with muscles. The equal-sized plates are roughly spindle-shaped with two long, lateral slits and smooth margins (Figure 18D, E). The slits are covered with a clear, hard layer that fractures easily when probed. The surface of the gizzard plates is textured with irregularly shaped polygons (Figure 18C). The esophagus does not expand into a crop posterior to the gizzard plates. The salivary glands are short.

The supraintestinal ganglion is located toward the anterior of the visceral loop, which is adjacent to, or adjoining, the fused pleural-parietal ganglion (Figure 17D).

The penial sac is barrel-shaped, and the tip of the papilla is hammer-shaped (Figure 17B). One lobe of the hammer is much shorter than the other lobe. The convoluted prostate branches to a short ejaculatory duct that is completely surrounded by the convoluted prostate.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figure 17C). The large mucous gland has one lobe, and the free end bends. Two small and spherical secondary bursae branch off the primary, thin-walled bursa copulatrix. In addition, two adjoined semispherical bodies lie near the intersection of the bursa copulatrix and the female gland.

Discussion: The gizzard plates are by far the most easily recognized features of *P. fenestra*. They are equal in size and shape, with two long slits; one slit is on each edge of the concave surface. The only other species with similar slits is *P. auriformis*, but those slits are smaller and shallower. Furthermore, *P. auriformis* is larger and has a prominent notch in the center of the posterior end of the posterior shield. *Philine infundibulum* and *P. sarcophaga* also have slits of the gizzard plates, but they occur only on two of the three unequal plates.

Philine fenestra has two spherical and appressed bodies between the secondary bursae and the receptaculum seminis. The penial papilla is small and rests on top of two additional penial lobes, similar to those found in *P. sarcophaga* and *P. paucipapillata* (identified as *P. orientalis* by Morton & Chiu, 1990).

Philine finmarchica M. Sars, 1878

(Figures 19, 20)

Philine finmarchica Sars, 1878: 296, pl. 18, fig. 10a–d; pl. 12, fig. 1a, b. Marcus, 1974: 352, figs. 88–92.

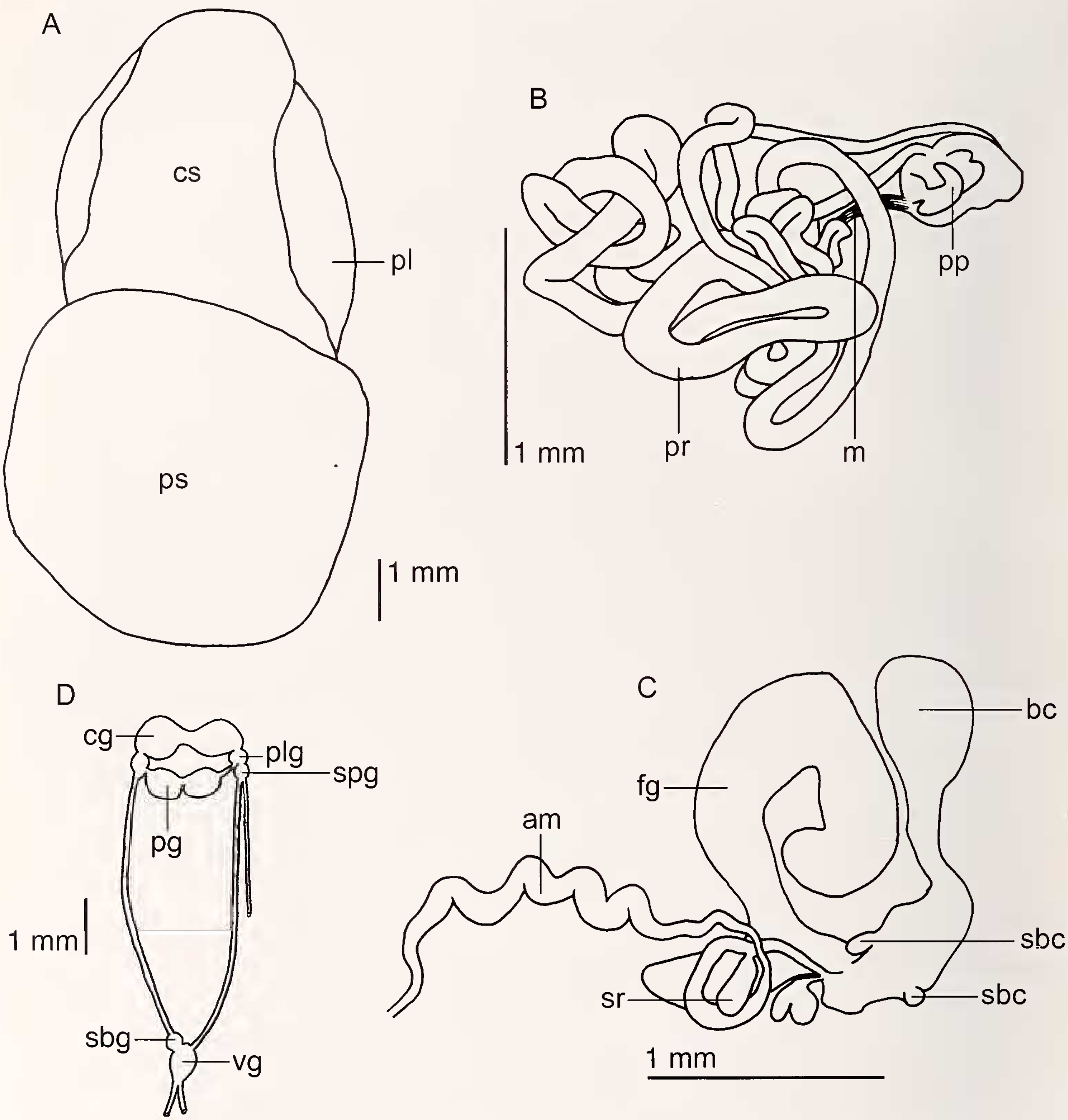

Figure 17. *Philine fenestra* (SAM FB 402A), anatomy: **A,** dorsal view of a preserved animal; **B,** male reproductive system; **C,** female reproductive system; **D,** nervous system. Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **cg,** cephalic ganglion; **cs,** cephalic shield; **fg,** female gland; **m,** muscle; **pg,** pedal ganglion; **pl,** parapodial lobe; **plg,** parietal-pleural ganglion; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbc,** secondary bursa copulatrix; **sbg,** subintestinal ganglion; **spg,** supraintestinal ganglion; **sr,** receptaculum seminis; **vg,** visceral ganglion.

Material: CASIZ 076660, one specimen, dissected, off Woods Hole, Massachusetts, 41°31′N, 70°40′W.

Distribution: This species is known from Cape Cod to Greenland, the eastern Atlantic and Arctic Ocean (Marcus, 1974).

External morphology: The preserved animals are uniformly white and approximately 2 cm long. The

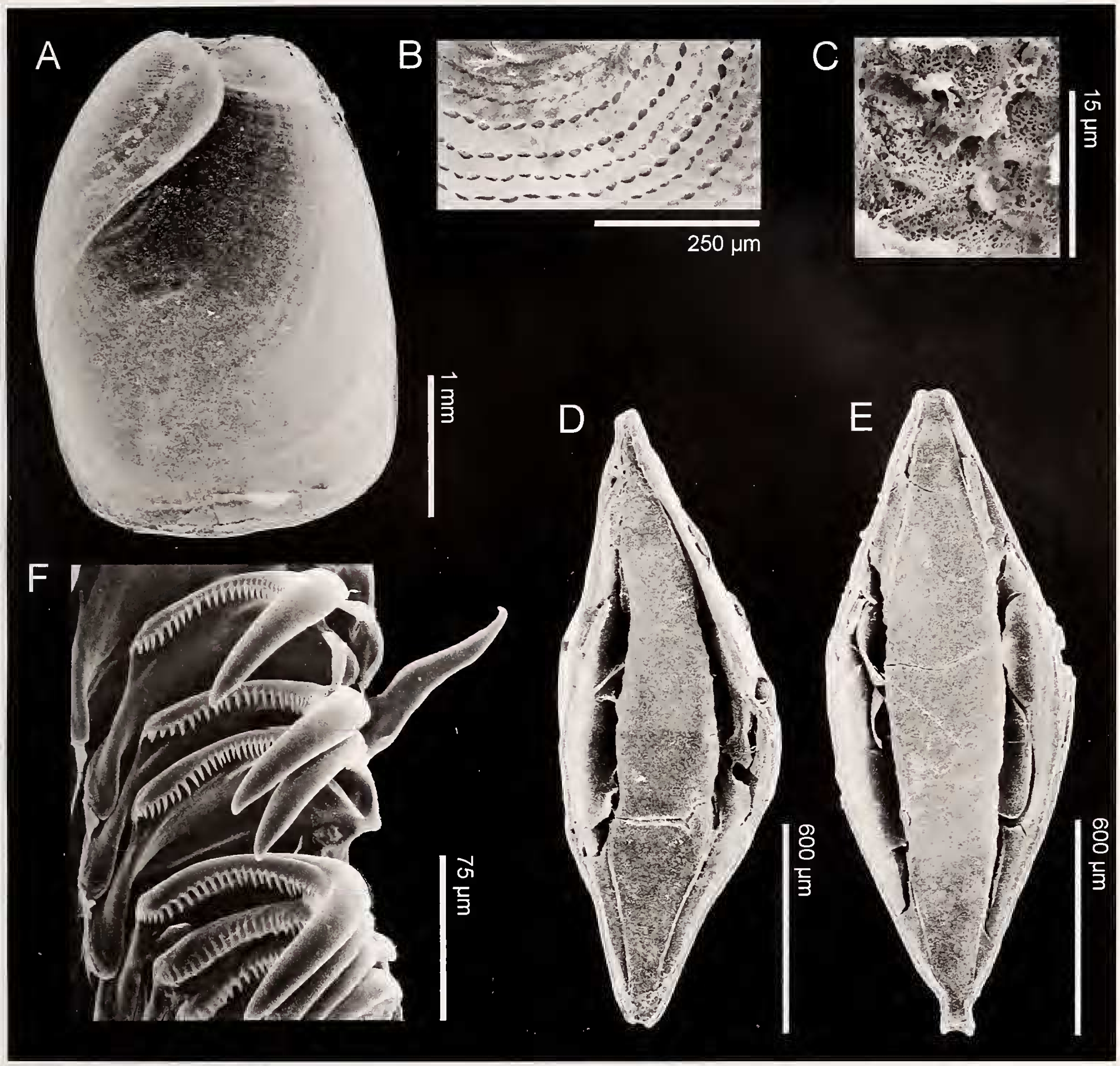

Figure 18. *Philine fenestra* (SAM FB 402A), SEM photographs of internal hard structures: **A**, ventral view of the shell; **B**, shell microsculpture; **C**, gizzard-plate microsculpture; **D**, **E**, gizzard plates; **F**, radular teeth.

cephalic and posterior shields are approximately the same size, and the parapodial lobes are narrow (Figure 19A). The posterior shield has a shallow notch.

Internal morphology: The shell is loosely coiled with a smooth surface.

There are two dorsal oral glands and one ventral oral gland. The radula has the formula of 15–16 × 1.0.1. The broad inner lateral teeth are covered with 72–80 elongate denticles. The esophagus does not expand into a crop posterior to the three, large, spindle-shaped and equal-sized gizzard plates. The gizzard is muscularized (Figure 19E), but the three large, equal-sized plates are not covered with muscles. The gizzard plates (Figure 20) lack pores and slits. The salivary glands are short.

The fused pleural-parietal ganglion is adjacent to the anterior supraintestinal ganglion (Figure 19C). The genital ganglion is fused to the visceral ganglion and adjacent to the subintestinal ganglion.

The penial papilla is hammer-shaped with lobes that are almost equal in size (Figure 19B). The ejaculatory

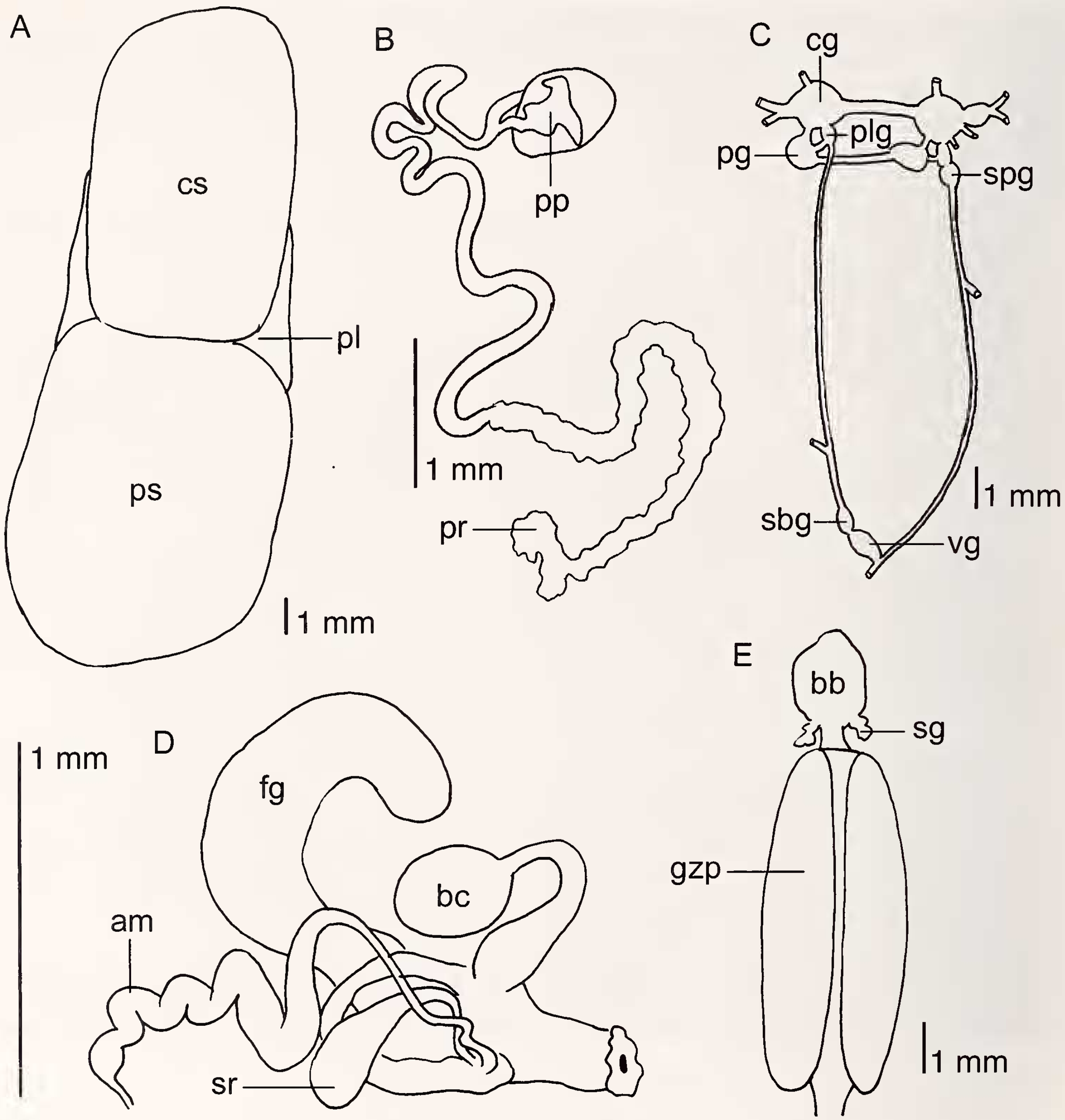

Figure 19. *Philine finmarchica* (CASIZ 076660) anatomy: **A,** dorsal view of a living animal; **B,** male reproductive system; **C,** nervous system; **D,** female reproductive system; **E,** anterior portion of the digestive system. Abbreviations: **am,** ampulla; **bb,** buccal bulb; **bc,** bursa copulatrix; **cg,** cephalic ganglion; **cs,** cephalic shield; **fg,** female glands; **gz,** gizzard plate; **pg,** pedal ganglion; **pl,** parapodial lobe; **plg,** parietal-pleural ganglion; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbg,** subintestinal ganglion; **sg,** salivary gland; **spg,** supraintestinal ganglion; **sr,** receptaculum seminis; **vg,** visceral ganglion.

duct has a very short branch that connects to the base of the penial papilla. The distal portion of the prostate is nodular, elongate, and simple. The convoluted ampulla (Figure 19D) narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis. The bursa copulatrix is large with a wide duct that joins the genital atrium. There is no secondary bursa copulatrix.

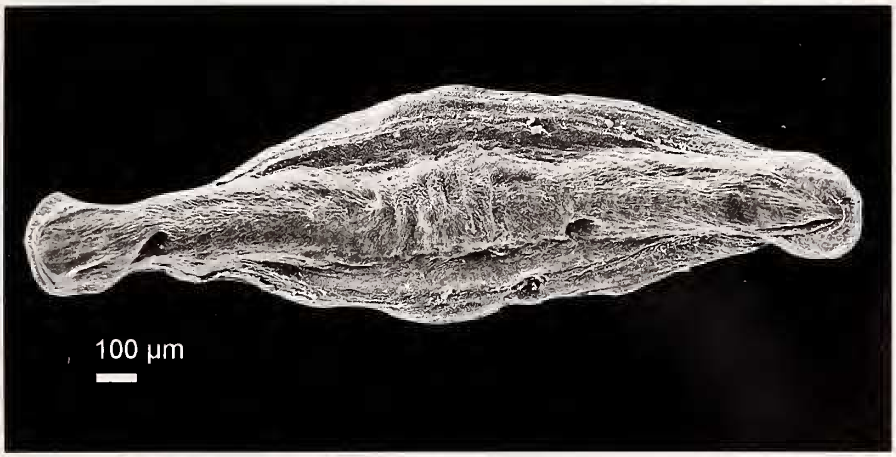

Figure 20. *Philine finmarchica* (CASIZ 076660). SEM photograph of a gizzard plate.

Discussion: *Philine finmarchica* lacks many of the characters shared by the other species within the *P. aperta* clade. The prostate, for example, is simple and nodular instead of convoluted and smooth, the gizzard plates are lenticular instead of spindle-shaped, and the gizzard plates lack slits or pores. However, the penial papilla illustrated here and by Marcus (1974:fig. 92) is clearly hammer-shaped with more or less equal lobes, similar in morphology to that of *P. aperta*. A very short ejaculatory duct is present, but it is much less developed than in any other member of the *P. aperta* clade.

Philine habei Valdés, 2008

(Figures 21, 22)

Philine habei Valdés, 2008:717–720, fig. 64A, 65B.

Material: MNHN (no specimen number), Station CP 15588, specimens (one dissected), 580–593 m, Tonga: Cheal nord Nomuka 20°10′S, 174°43′W.

Distribution: *Philine habei* is known from New Cale-

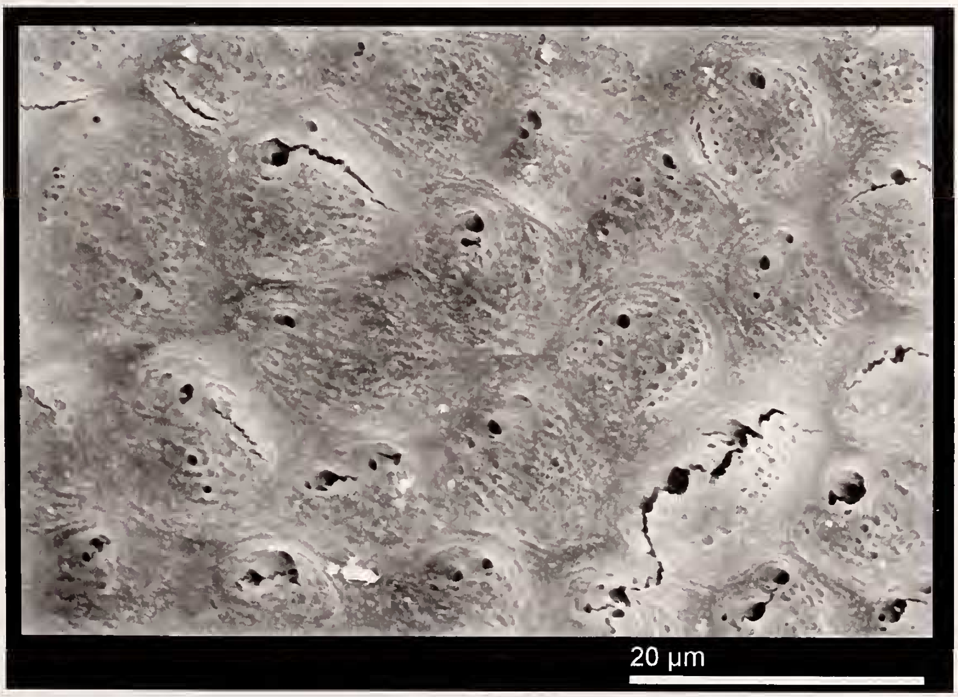

Figure 21. SEM photograph of the gizzard-plate microsculpture of *P. habei* (MNHN no specimen number).

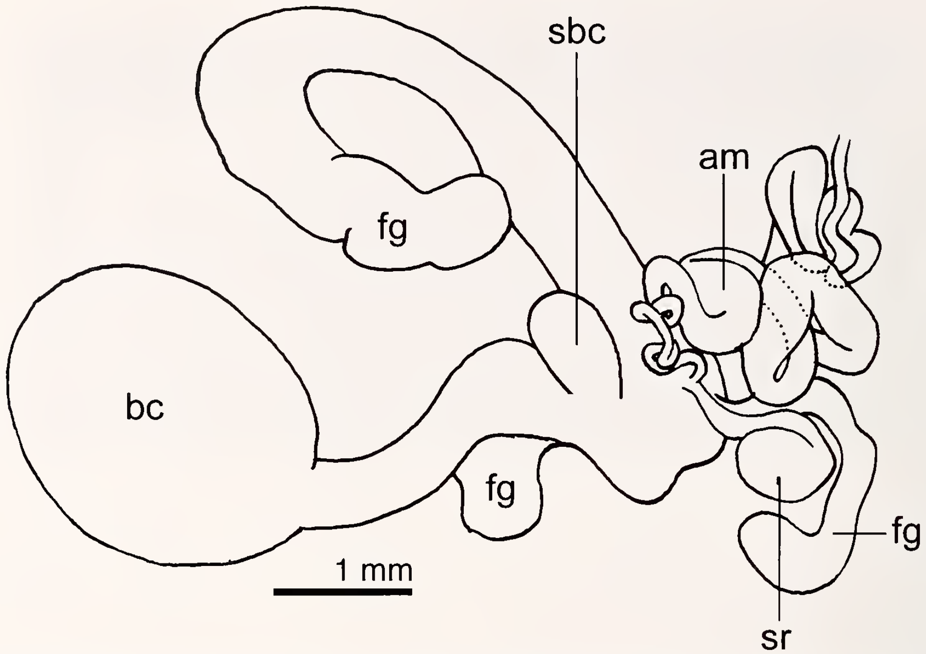

Figure 22. Female reproductive organs of *P. habei* (MNHN no specimen number). Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **fg,** female glands; **sbc,** secondary bursa copulatrix; **sr,** receptaculum seminis.

donia, Fiji, Tonga, Vanuatu, and Wallis and Futuna Islands from 250–688 m. The type locality is in Fiji.

External morphology: The living animal is uniformly white and approximately 3 cm long. The cephalic shield is slightly longer than the posterior shield. The posterior shield lacks a posterior notch. The parapodial lobes are narrow.

Internal morphology: The shell is particularly fragile and lacks punctation. It has a high rate of expansion.

There are no dorsal or ventral oral glands. The buccal bulb is small. The radular formula is 16 × 1.0.1. The lateral teeth have a broad base that lacks denticles. The crop is indistinct. The gizzard is muscularized, but the plates are not covered with muscles. The spindle-shaped gizzard plates all have two large pores; their margins are smooth. The unpaired plate is smaller than the paired plates. The plate microsculpture consists of a meshwork of irregularly shaped polygons (Figure 21). The salivary glands are small.

The fused pleural-parietal ganglion is adjacent to the anterior supraintestinal ganglion. The genital ganglion remains distinct from the visceral ganglion, but the visceral ganglion is fused to the subintestinal ganglion.

The hammer-shaped penial papilla has markedly unequal lobes, is supported by a stout stalk, and distends the base of the pyriform penial sac over the convoluted prostate. The convoluted prostate branches to the ejaculatory duct, and a short muscle connects the end of the prostate to the sac. The ejaculatory duct is short, but it is not surrounded by the convoluted prostate.

The convoluted ampulla narrows into the hermaphroditic duct (Figure 22), at the side of which branches the single receptaculum seminis. The large mucous gland has two lobes. There is one secondary bursa copulatrix.

Discussion: *Philine habei* (Valdés, 2008), along with *P. puka*, has large, elongate pores on the gizzard plates. The plate microstructure in *P. habei* however lacks the many indentations present in *P. puka. Philine habei* differs from *P. puka* in that it lacks denticles on the inner lateral teeth.

The penial papilla is similar to that found in *P. argentata* and *P. quadripartita* because of the unequal lobes on the large hammer head and an additional lobe branching from the base of the stalk.

Philine infundibulum Dall, 1889

(Figures 23, 24)

Philine infundibulum Dall, 1889:57. Marcus, 1974:355, figs. 93–97.

Material: CASIZ 079484, one specimen, dissected, off Woods Hole, Massachusetts. CASIZ 076159, one specimen, dissected, off Woods Hole.

Distribution: Known from the western Atlantic from

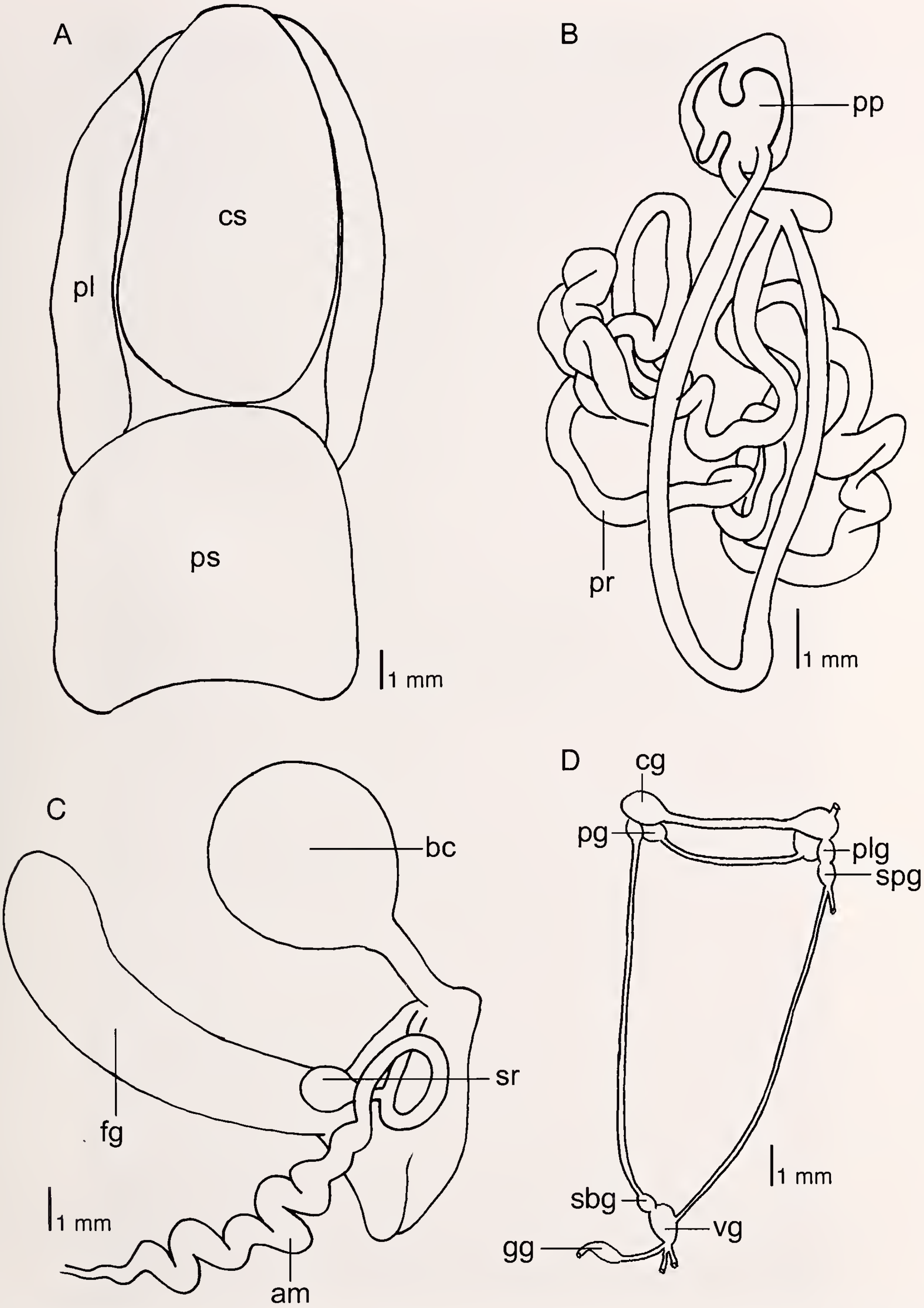

Figure 23. *Philine infundibulum* (CASIZ 076159), anatomy: **A**, dorsal view of a living animal; **B**, male reproductive system; **C**, female reproductive system; **D**, nervous system; **E**, anterior portion of the digestive system. Abbreviations: **am**, ampulla; **bb**, buccal bulb; **bc**, bursa copulatrix; **cg**, cephalic ganglion; **cs**, cephalic shield; **fg**, female glands; **gz**, gizzard; **m**, muscle; **og**, oral gland; **pg**, pedal ganglion; **pl**, parapodial lobe; **plg**, parietal-pleural ganglion; **pp**, penial papilla; **pr**, prostate; **ps**, posterior shield; **sbg**, subintestinal ganglion; **sg**, salivary gland; **spg**, supraintestinal ganglion; **sr**, receptaculum seminis; **vg**, visceral ganglion.

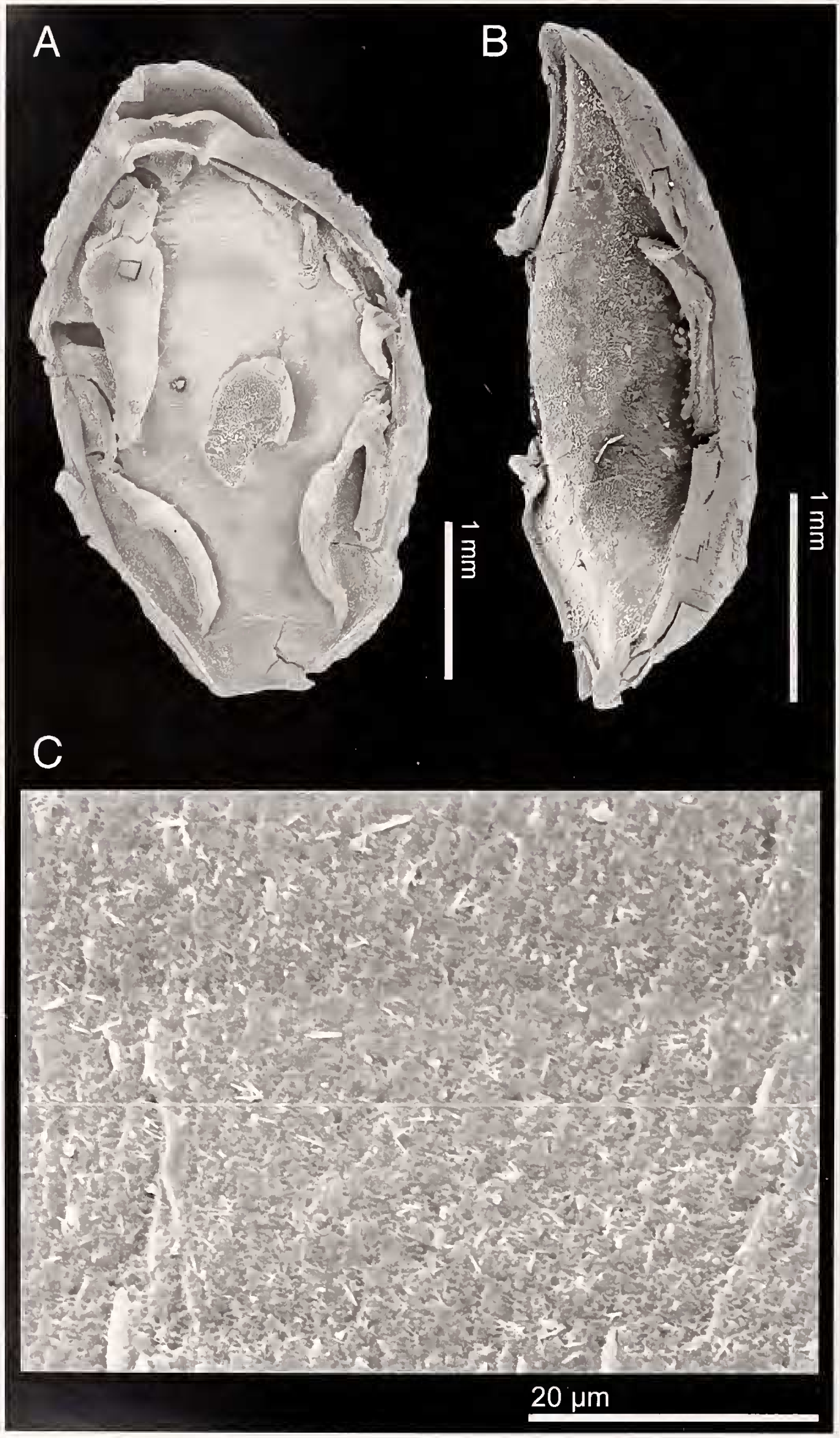

Figure 24. *Philine infundibulum* (CASIZ 076159), SEM photographs of internal hard structures: **A,** paired gizzard plate; **B,** unpaired gizzard plate; **C,** gizzard-plate microsculpture.

northern Brazil to Cape Cod, Massachusetts (Marcus, 1974; present study).

External morphology: The preserved animals are uniformly white and approximately 3 cm long (Marcus & Marcus, 1967). The cephalic shield is longer than the posterior shield (Figure 23A). The parapodial lobes are thin and flimsy. It is uncertain whether the posterior shield is notched or unnotched in the two dissected specimens.

Internal morphology: The smooth shell is relatively tightly coiled for a *Philine*.

There are two dorsal oral glands and one ventral oral gland. The buccal bulb and radula are reduced, and the radular formula is 20–24 × 1.1.0.1.1, with 28–37 denticles on the inner side of the broad tooth. The radula of the present specimen was not examined by SEM because it was already mounted on a microscope slide. The crop is indistinct. The gizzard is muscularized, but the three large plates are not covered with muscles. The paired plates (Figure 24B) are spindle-shaped with a single large slit on the concave edge. The unpaired plate (Figure 24A) is slightly smaller than the other two; it is rhomboidal and lacks slits. The high magnification of the gizzard plates reveals that they lack any obvious microstructure (Figure 24C). The salivary glands are short.

The fused pleural-parietal ganglion is adjacent to the anterior supraintestinal ganglion (Figure 23D). The genital ganglion remains distinct from the visceral ganglion, but the visceral ganglion is fused to the subintestinal ganglion.

The hammer-shaped penial papilla has subequal lobes and rests within the penial sac (Figure 23B). The ejaculatory duct branches from the convoluted prostate branches, and a short muscle connects the end of the prostate to the sac. The ejaculatory duct is long, but it is not surrounded by the convoluted prostate. The prostate is smooth.

The convoluted ampulla narrows into the hermaphroditic duct (Figure 23C), at the side of which branches a single, long and narrow receptaculum seminis. The female gland is relatively small for this clade. The bursa copulatrix is large, and there is a single secondary bursa copulatrix.

Discussion: The simple, hammer-shaped penial papilla is most similar to that of *P. auriformis* because the lobes are subequal and small, resting on a short stalk. The plates are all spindle-shaped and lack pores. The paired plates are more tapered than the unpaired, and as in *P. sarcophaga*, one edge is much flatter than the other edge. They also have a single large slit on the edge of the rounded side. *Philine sarcophaga* and *P. fenestra* also have slits, but the slits in *P. fenestra* are all of the same size, and they line the edges of all three equally sized plates. *Philine infundibulum* is more similar to *P. sarcophaga*, which also has two paired plates. The unpaired plate in both of these species is rhomboidal, but the plate in *P. infundibulum* lacks the rounded anterior knob present in *P. sarcophaga*.

The gizzard-plate microstructure in *P. infundibulum* is difficult to interpret because our specimen is poorly preserved.

Philine orientalis A. Adams, 1854

(Figures 2E, 25–29)

Philine orientalis A. Adams in Adams and Adams, 1854–1858:94.
Philine argentata Gould, 1859: 139 syn. nov.
Philine japonica Lischke, 1872: 105, syn. nov.
Philine striatella Tapparone-Canefri, 1874:109, syn. nov.

Material: Types of *P. orientalis*, BMNH, H. Cuming collection, accession 1829, shell and gizzard plates, "eastern seas." CASIZ 078442, nine specimens, two dissected, 1 m depth on sand bar at night, 100 m E of Matiara Hotel, Langkawi Island, Strait of Malacca, Malay Peninsula, Malaysia, 6°26′N, 99°48′E, collected by T. M. Gosliner. BMNH 1996409, three specimens (all dissected), Nagasaki, Japan. CASIZ 082054, 20 specimens, one dissected, 80–100 fathoms, southwest of Kao-Hsiung into South China Sea, Taiwan, October 12, 1972, collected by F. B. Steiner. CASIZ 174126, four specimens, two dissected, Bodga Harbor, California, July 1998, Michelle Chow.

Distribution: *Philine orientalis* was originally described from "eastern seas," whereas *P. argentata* was described from Hakodate Bay, Japan, 2–6 fathoms. It is also known from Malaysia, Japan, and Taiwan, and it has been introduced in central California (present study).

External morphology: The living animal is uniformly white (Figure 2E) and approximately 2.5–4 cm in length. The cephalic shield is longer than the posterior shield, and the parapodial lobes are thick and muscular (Figures 25A, 26A). A notch may be present or absent on the posterior shield but seems to be absent in poorly preserved specimens.

Internal morphology: The shell is loosely to tightly coiled and is either smooth or punctate with an ovate perimeter (Figures 27A, B; 28A, B; 29A).

There are two appressed ventral oral glands, and two dorsal oral glands. The buccal mass is small, and the radula has the formula 17–22 × 1.0.1, with 35–42 small denticles on the broad inner lateral tooth (Figures 28E, 29E). There is no crop. The gizzard is muscularized, although the plates are not covered with muscles

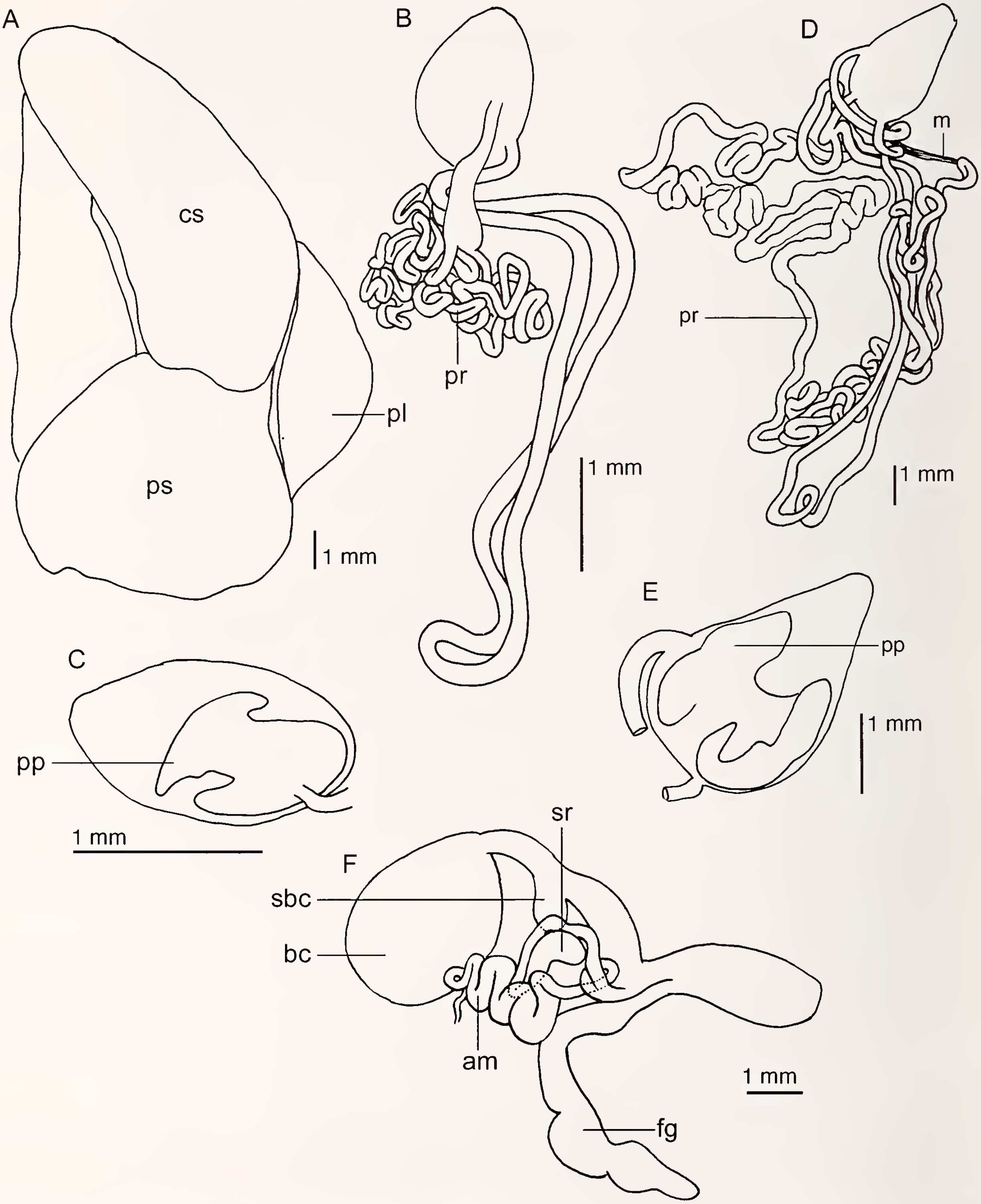

Figure 25. *Philine orientalis* anatomy, specimens from Nagasaki, Japan (BMNH 1996409 [A–C, F]) and Tomales Bay, California (CASIZ 082054 [D, E]). **A,** dorsal view of a living animal; **B,** male reproductive system; **C,** penis; **D,** male reproductive system; **E,** penis; **F,** female reproductive organ. Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **cs,** cephalic shield; **fg,** female glands; **m,** muscle; **pl,** parapodial lobe; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbc,** secondary bursa copulatrix; **sr,** receptaculum seminis.

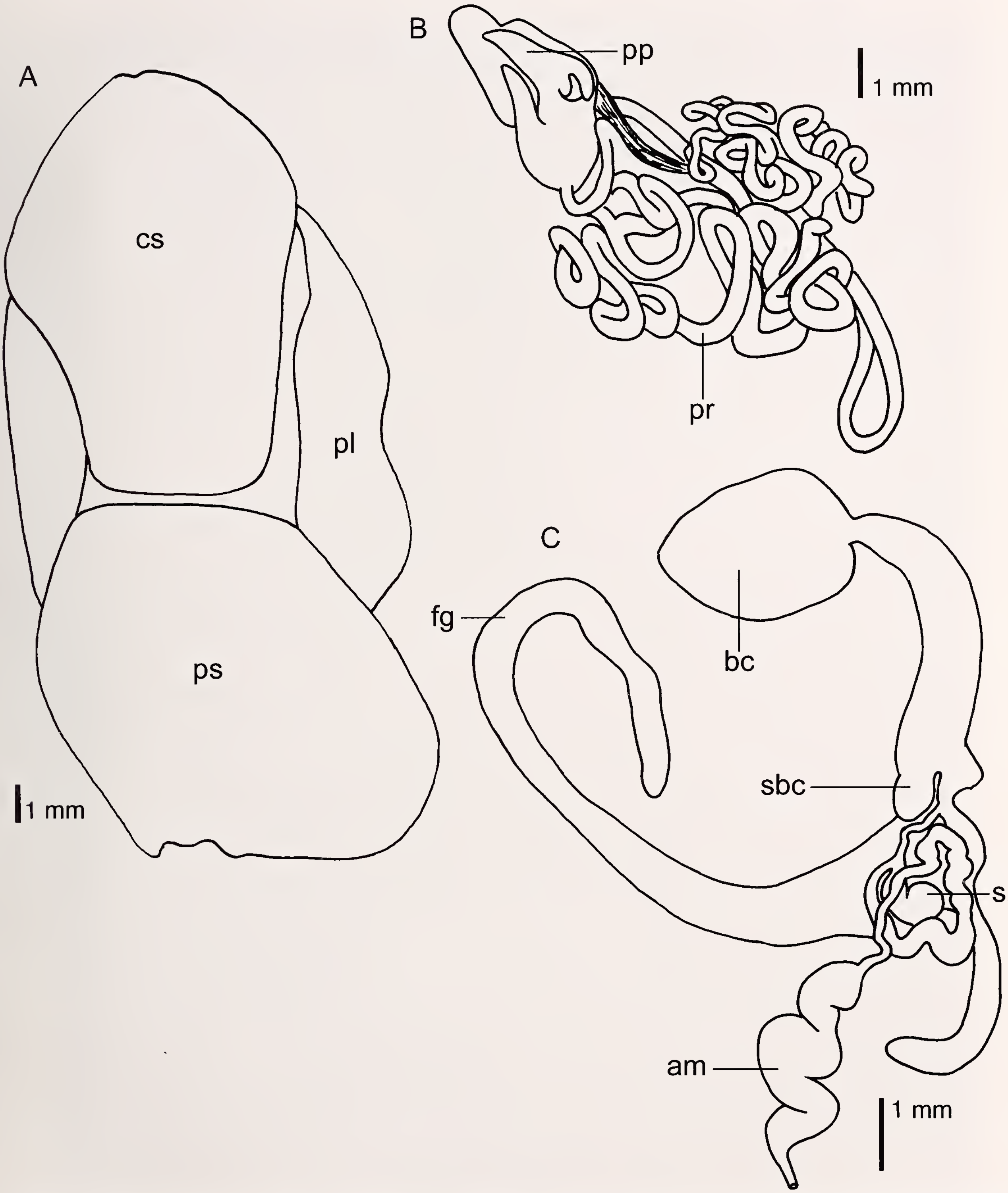

Figure 26. *Philine orientalis* anatomy, specimen from Malaysia, CASIZ 078442: **A,** preserved animal; **B,** penis; **C,** female reproductive system. Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **cs,** cephalic shield; **fg,** female glands; **pl,** parapodial lobe; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbc,** secondary bursa copulatrix; **sr,** receptaculum seminis.

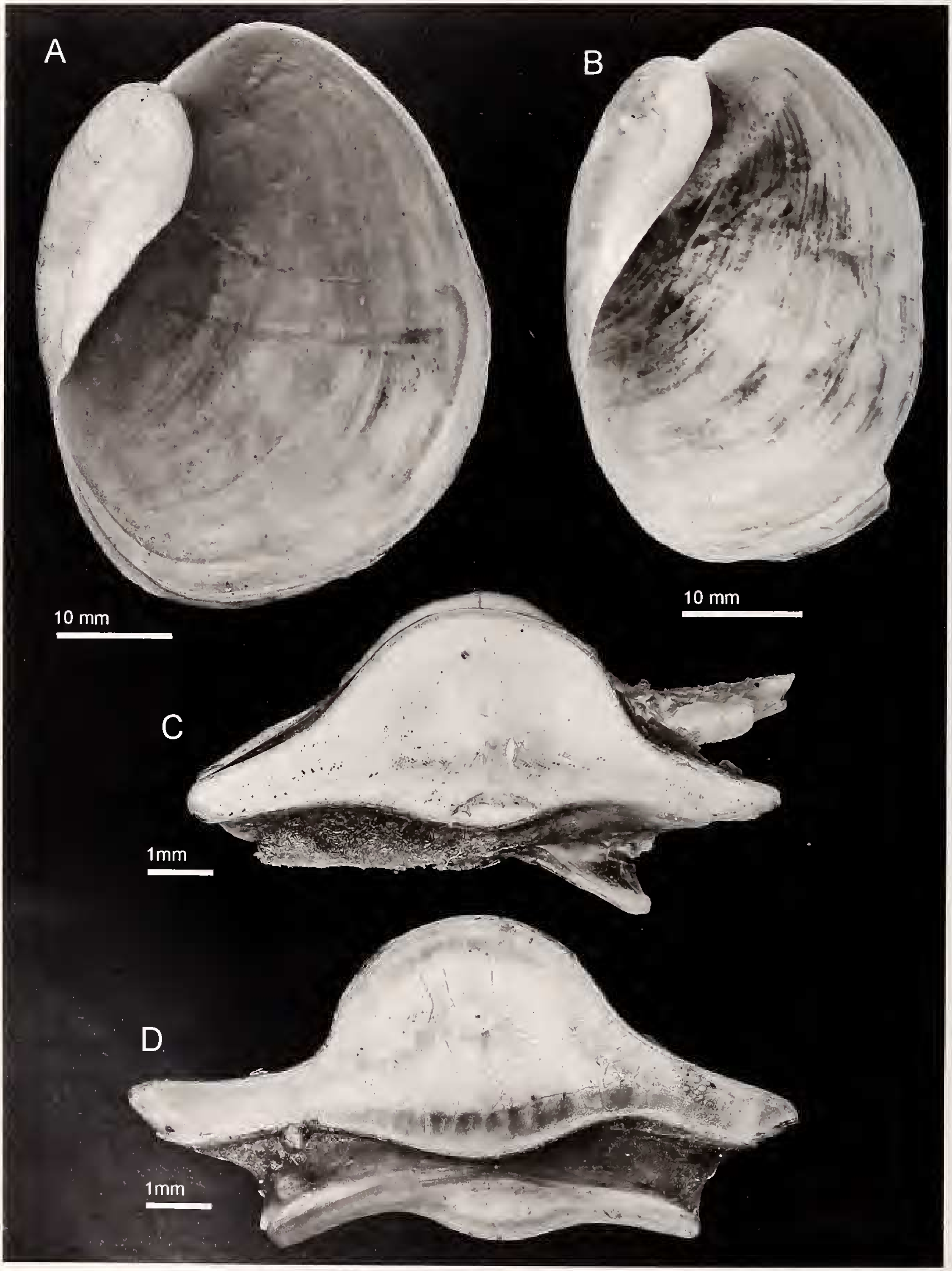

Figure 27. *Philine orientalis*, light photographs of the type specimens, BMNH, H. Cuming collection, accession number 1829. **A, B,** ventral view of the shells; **C, D,** gizzard plates.

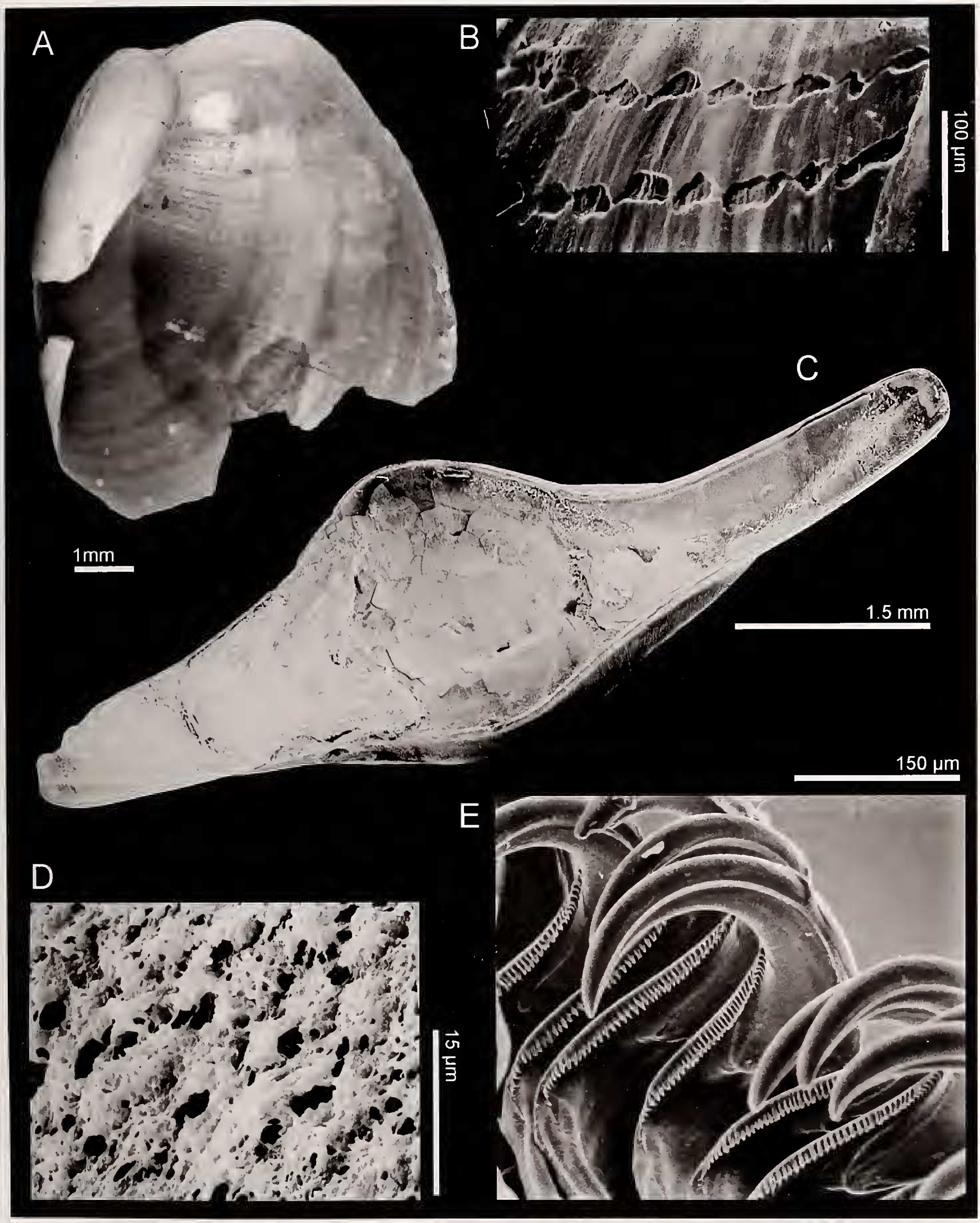

Figure 28. *Philine orientalis* (BMNH 199609), specimen from Nagasaki, Japan, photographs of internal hard structures. **A,** light photograph of a ventral view of the shell; **B,** SEM photograph of the shell microsculpture; **C,** SEM photograph of a gizzard plate; **D,** SEM photograph of the gizzard-plate microsculpture; **E,** SEM photograph of the radular teeth.

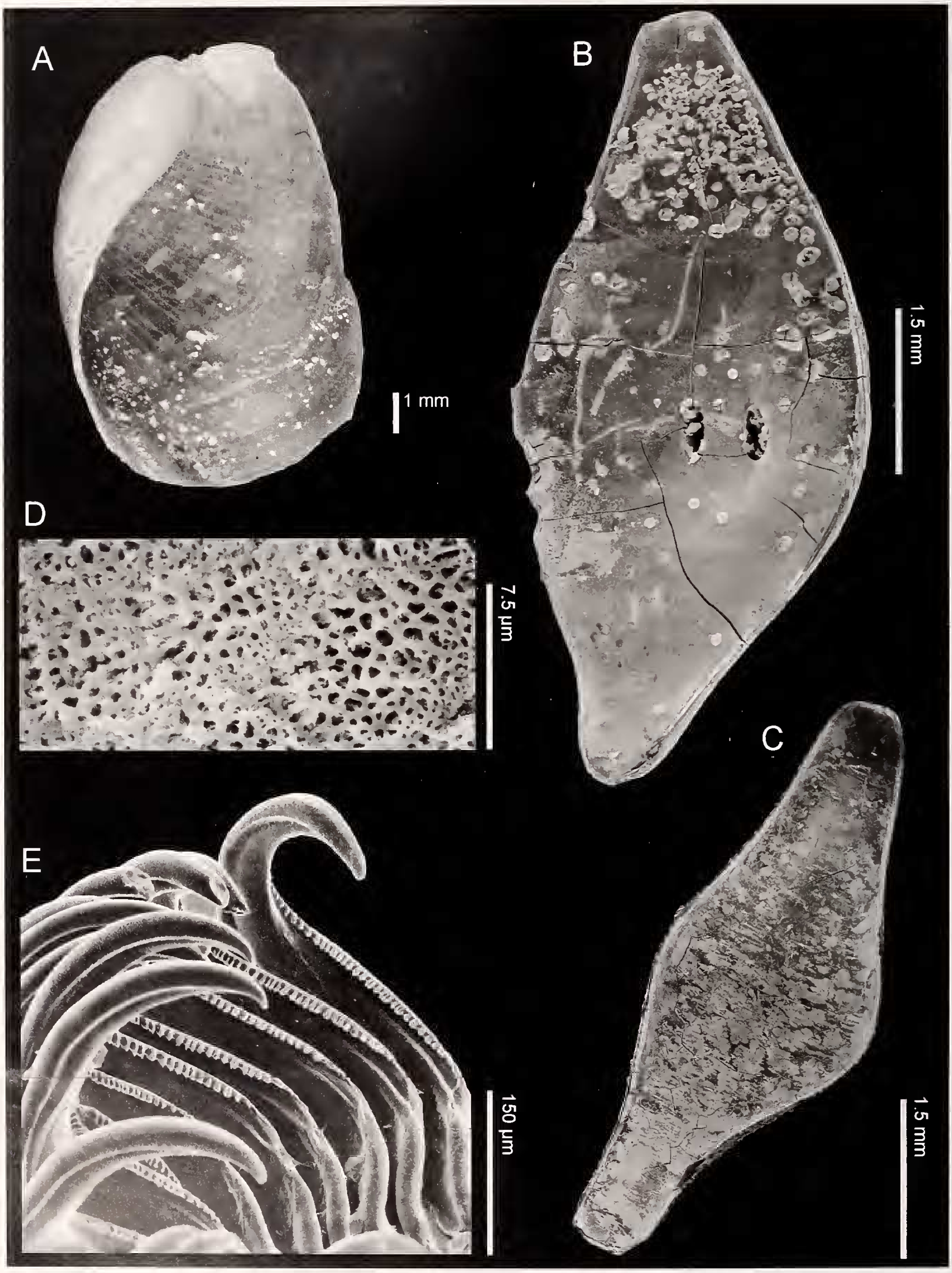

Figure 29. *Philine orientalis* (CASIZ 174126), specimen from Bodega Harbor, California, photographs of internal hard structures: **A,** light photograph of a ventral view of the shell; **B,** SEM photograph of a paired gizzard plate; **C,** SEM photograph of the unpaired gizzard plate; **D,** SEM photograph of the gizzard-plate microstructure; **E,** SEM photograph of the radular teeth.

(Figure 27C, D). The three spindle-shaped plates have small-to-medium, shallow pores (Figures 27C, D; 28C; 29B, C). The two paired plates are broad and fill the entire anterior portion of the body. The unpaired plate is much shorter and narrower. The microsculpture consists of regularly arranged polygons (Figures 28D, 29D). The salivary glands are short.

The supraintestinal ganglion is located toward the anterior of the visceral loop and is adjacent to the fused pleural-parietal ganglion. The osphradial nerve branches off halfway between the supraintestinal ganglion and the visceral ganglion. The subintestinal ganglion is fused to the visceral ganglion, but the genital ganglion remains distinct.

The penial sac is ovoid, and the penial papilla is hammer-shaped with subequal lobes and is supported above the cushion-shaped base by a stalk (Figures 25C, E; 26B). The base of the penial papilla does not distend the wide penial sac. The convoluted prostate branches into a long ejaculatory duct that extends to, or far beyond, the buccal mass to the gizzard, but it is completely uncovered by the prostate (Figures 25B, D; 26B). The prostate seems especially granular.

The convoluted ampulla narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis (Figures 25F, 26C). The large mucous gland has one lobe above the albumen gland, and the free end bends. There is a single secondary bursa copulatrix.

Discussion: There has been much confusion surrounding the identification of *P. orientalis*, based largely on the facts that the type material was described only as collected from the vague locality "eastern seas" and that no complete description of the anatomy had been published. The type material in the BMNH consists of a shell and three gizzard plates. The material agrees with specimens we have studied here from Japan, Malaysia, Taiwan, and California. All of these specimens have two large paired gizzard plates and a narrow, shorter unpaired plate.

The pore size on the gizzard plates of this species are more variable than those of any of the other species we have described. The type specimens (Figure 27C, D), the Malaysian specimens that we have studied, and the Japanese specimens that we have studied (e.g., Figure 28C) have small pores. However, the specimen from Bodega Harbor, California, that we depict in Figure 29B has slightly larger pores on the paired plates.

Philine orientalis is the oldest available name for these taxa, and *P. argentata* and its synonyms should be regarded as junior synonyms of *P. orientalis*. We agree with other authors who have synonymized *P. argentata*, *P. japonica*, and *P. striatella* (e.g., Kuroda et al., 1971). Although the descriptions of these taxa are largely incomplete, there seems to be a single large, shallow-water species in Japanese waters, the type locality of all three species. It seems that *P. orientalis* has been introduced into San Francisco Bay and the nearby estuaries of Tomales Bay and Bodega Bay, and it was first recorded by Gosliner & Williams (2007) as *P.* sp. As with *P. auriformis*, this species was probably introduced by discharge of ballast water.

Specimens identified as *P. orientalis* from Hong Kong (Morton & Chiu, 1990) and Cambodia (present study) are morphologically distinct from those found in Malaysia, Japan, and Taiwan (present study) and represent a distinct species described here as *P. paucipapillata*. Throughout the Pacific waters of Southeast Asia, there seem to be two distinct members of the *Philine aperta* clade: *P. orientalis* and *P. paucipapillata*. The gizzard plates of *P. orientalis* have two smaller pores, similar to those in *P. paucipapillata* from Hong Kong and Cambodia, but the ends of the spindle are proportionately much longer in *P. orientalis*. Both have the regular polygon microstructure of the gizzard plates. The penial papilla of *P. orientalis* has two hammer-shaped subequal lobes similar to that of *P. habei* (Valdés, 2008) and *P. quadripartita*, but it differs markedly from that of *P. paucipapillata*. In that species, the penial papilla is rounded without the two elaborate hammer-shaped arms found in *P. orientalis*.

The specimen of *P. argentata* described in Habe (1950) as *Yokoyamaia argentata*, has a "hint of spines that are extensions of shell ribs" (Gosliner, 1988). Habe's material is most likely a different species.

Philine paucipapillata Price, Gosliner, and Valdés, sp. nov.

(Figures 30, 31)

Philine orientalis Adams and Adams, 1854–1858: 39, Morton and Chiu, 1990:289, figs. 3, 4, misidentification.

Type material: Holotype, CASIZ 174143, Kampote and Prek Romeas, Cambodia, fish landings, March 29 and April 6, 2006, Tyson Roberts. Paratypes, CASIZ 174144, three specimens, one dissected, Kampote and Prek Romeas, Cambodia, fish landings, March 29 and April 6, 2006, Tyson Roberts.

Additional material: BMNH 1996410, more than 10 specimens, dissected, Tolo Channel, Hong Kong, collected by J. D. Taylor.

Distribution: Known from Tolo Channel, Hong Kong (Morton & Chiu, 1990) and Cambodia (present study).

Etymology: The name *paucipapillata* refers to the fact that this species has a penial papilla that is much smaller than that of other members of this clade.

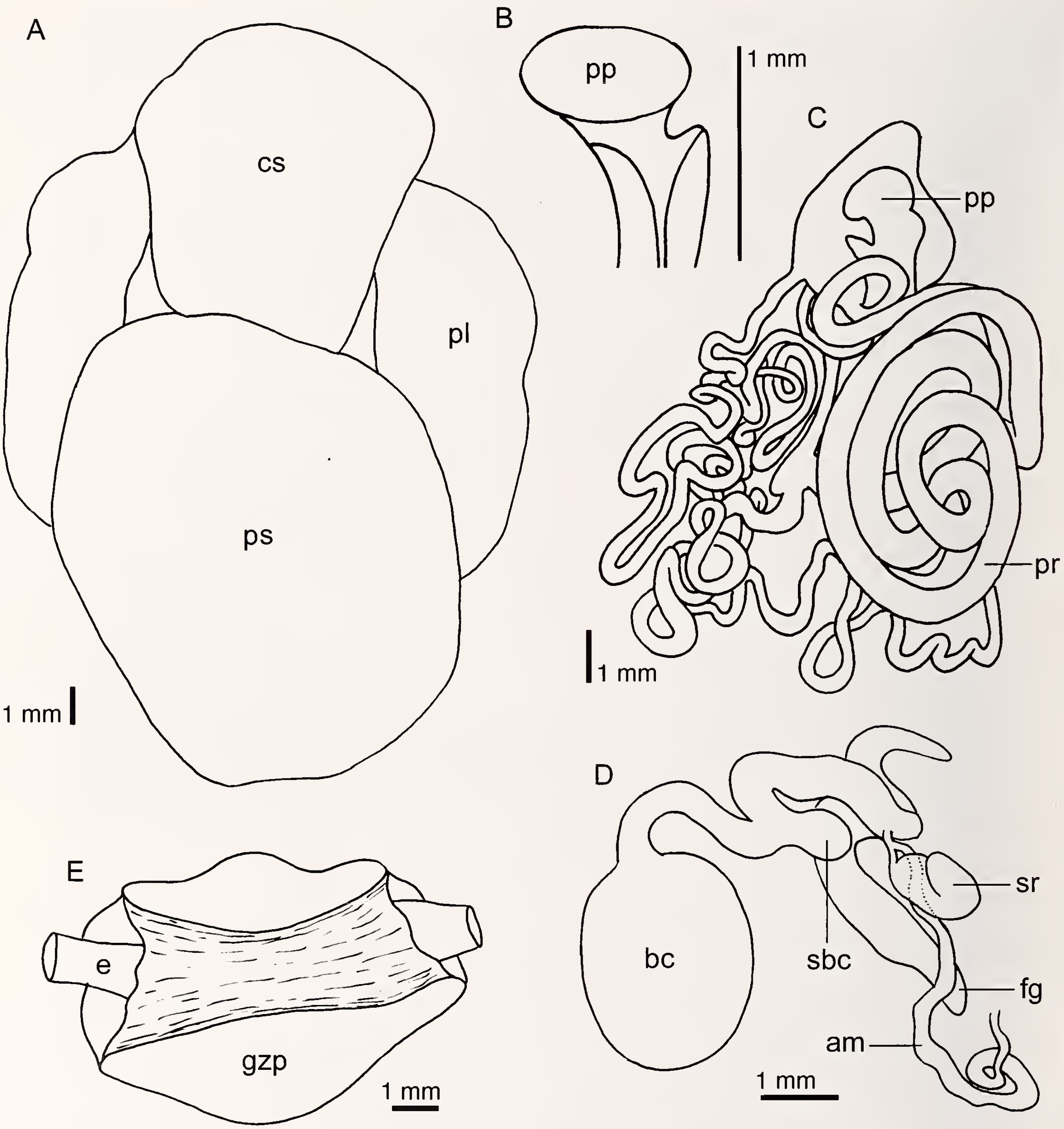

Figure 30. *Philine paucipapillata* (BMNH 1996410), anatomy: **A,** dorsal view of a preserved animal; **B,** penis; **C,** male reproductive system; **D,** female reproductive system; **E,** gizzard. Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **cs,** cephalic shield; **e,** esophagus; **fg,** female glands; **gzp,** gizzard plate; **pl,** parapodial lobe; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbc,** secondary bursa copulatrix; **sr,** receptaculum seminis.

Type locality: Kampote and Prek Romeas, Cambodia.

External morphology: The living animal is uniformly white and about 4–5 cm in length. The cephalic shield is longer than the posterior one (Figure 30A). The parapodial lobes are thick and muscular, and the posterior notch is very shallow to absent.

Internal morphology: The shell (Figure 31A) is tightly

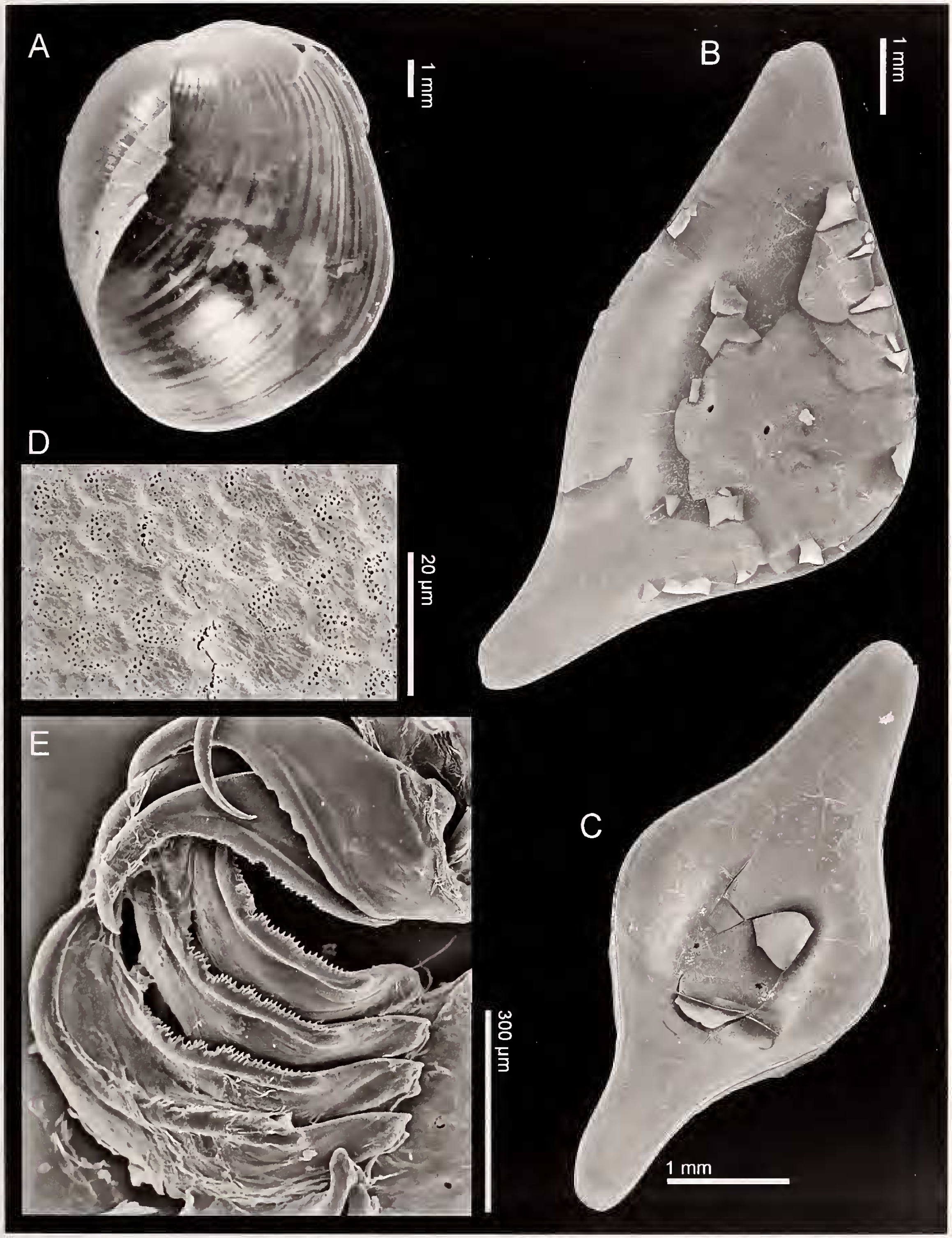

Figure 31. *Philine paucipapillata* (BMNH 1996410), photographs of internal hard structures: **A,** light photograph of a ventral view of the shell; **B,** SEM photograph of a paired gizzard plate; **C,** SEM photograph of the unpaired gizzard plate; **D,** SEM photograph of the gizzard-plate microsculpture; **E,** SEM photograph of the radular teeth.

coiled for a *Philine* and has an ovate perimeter. The surface of the shell is smooth.

There are two, appressed ventral oral glands and two dorsal oral glands. The buccal mass is small, and the radula has the formula 18–22 × 1.0.1. The broad inner lateral tooth (Figure 31E) has 38–40 denticles that are arranged in an irregular manner, with an uneven edge that undulates along the masticatory margin. There is no crop. The gizzard (Figure 30E) is muscularized, although the plates are not covered with muscles. The three spindle-shaped plates have minute, shallow pores (Figure 31B, C). The two paired plates (e.g., Figure 31B) are broad and fill the entire anterior portion of the body. The unpaired plate (Figure 31C) is much narrower. The plate microsculpture (Figure 31D) consists of irregularly shaped polygons. The salivary glands are short.

The supraintestinal ganglion is adjacent to the fused pleural-parietal ganglion. The osphradial nerve branches off from halfway between the supraintestinal ganglion and the visceral ganglion. The genital ganglion is distinct. The subintestinal ganglion is fused to the visceral ganglion.

The penial sac is ovoid, and the penial papilla is hammer-shaped but with short rounded lobes giving the entire papilla a club-shaped appearance (Figure 30B, C). The base of the papilla rests on two lobes that form the base of the penis. The tightly coiled prostate branches to the ejaculatory duct. The ejaculatory duct is highly convoluted. Its posterior end is connected to the penial sac by a short muscle. The prostate is smooth rather than granular.

The convoluted ampulla narrows into the hermaphroditic duct (Figure 30D), at the side of which branches the single receptaculum seminis. The large mucous gland has two lobes above the albumen gland, and the free ends bend. There is single secondary bursa copulatrix.

Discussion: This new species has been previously considered as *P. orientalis* (Morton & Chiu, 1990), but the distinctions in the bulbous penial papilla and the undulating denticular margin on the masticatory border of the inner lateral teeth clearly indicate that it is a distinct species. These important characters distinguish this species from all other described *Philine*.

Philine puka Price, Gosliner, and Valdés, sp. nov.

(Figures 32, 33)

Type material: Type material: Holotype: CASIZ 175005, one specimen, 200 m depth, Ewa, off the coast of Barbers Point, Oa'hu, Hawai'i, collected April 27, 1973 by D. Bonar. Paratypes: CASIZ 082128, three specimens, two dissected, 200 m depth, Ewa, off the coast of Barbers Point, Oa'hu, Hawai'i, collected April 27, 1973 by D. Bonar. CASIZ 081997, one specimen, United States Fisheries Commission Steamer *Albatross*, ST. D4045, off Kawaihae Light, Hawai'i. Hawai'ian Islands, 269–363 m depth, July 11, 1902. CASIZ 081995, one specimen, United States Fisheries Commission Steamer *Albatross*, ST. D3938, off Laysan Island Light, Hawai'ian Islands, 271–298 m depth, May 16, 1902. CASIZ 081993, one specimen, United States Fisheries Commission Steamer *Albatross*, ST. D3813, off Diamond Head Light, Oah'u. Hawai'ian Islands, 269–363 m depth, March 28, 1902

Distribution: This species is known only from deeper water off Laysan, Oa'hu and Hawai'i in the Hawai'ian Islands.

Etymology: The name puka, which is Hawai'ian for *hole*, refers to the large pores on the gizzard plates.

Type locality: Oah'u, Hawai'i.

External morphology: The preserved specimens are uniformly white and about 1 cm in length. The cephalic and posterior shields are approximately equal (Figure 32A). The parapodial lobes are thin, and the posterior notch is deep.

Internal morphology: The shell (Figure 33A) is loosely coiled for a *Philine*, and it has an ovate perimeter. The surface of the shell is smooth.

There is one, short ventral oral gland, and there are two dorsal oral glands. The buccal mass is small, and the radula has the formula 20 × 1.0.1 in the two specimens we examined. The broad inner lateral tooth has 39–44 denticles (Figure 33E). There is no crop. The gizzard is muscularized, although the plates are not covered with muscles. The three spindle-shaped plates have large, deep pores (Figure 33C, D). The unpaired plate (Figure 33C) is smaller than the other two (Figure 33D). The plate microsculpture (Figure 33B) consists of regularly arranged polygons, and there is a distinct pattern within each shape. The salivary glands are short.

The nervous system is euthyneurous. The supraintestinal ganglion is adjacent to the fused pleural-parietal ganglion (Figure 32E). The osphradial nerve branches off from halfway between the supraintestinal ganglion and the visceral ganglion. The genital ganglion is distinct.

The penial sac is rectangular, and the penial papilla is hammer-shaped. The base of the papilla is small and has two lobes (Figure 32B). The basal lobe of the hammer is much shorter than the other lobe. The longer lobe is slightly convoluted. The prostate branches (Figure 32C) to the ejaculatory duct, and the posterior end is not connected to the penial sac. The ejaculatory duct is relatively short, and it is not surrounded by the prostate.

The convoluted ampulla narrows (Figure 32D) into

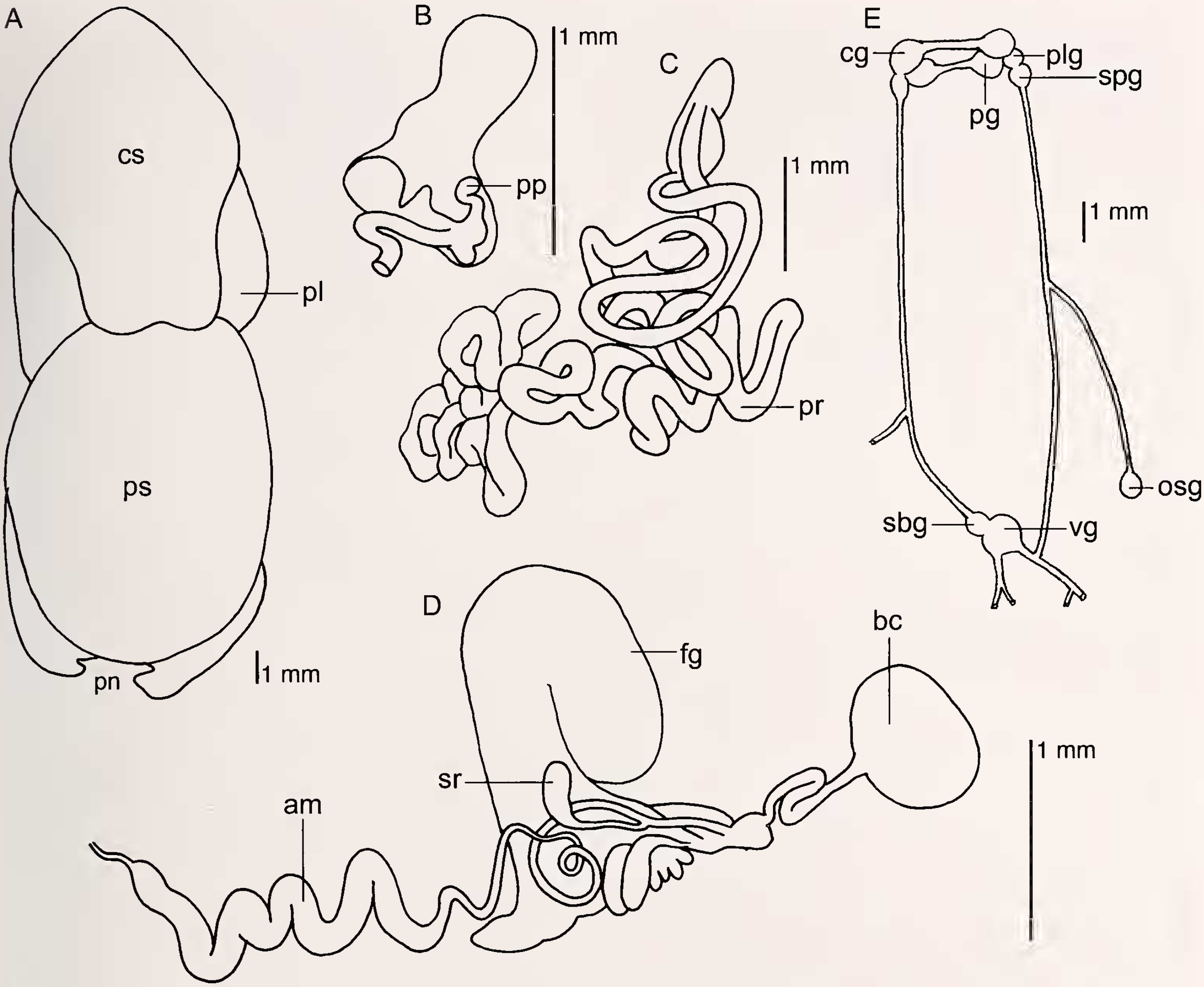

Figure 32. *Philine puka* (CASIZ 082128), anatomy: **A,** dorsal view of a preserved animal; **B,** penis; **C,** male reproductive system; **D,** female reproductive system; **E,** nervous system. Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **cg,** cephalic ganglion; **cs,** cephalic shield; **fg,** female glands; **osg,** osphradial ganglion; **pg,** pedal ganglion; **pl,** parapodial lobe; **plg,** parietal-pleural ganglion; **pn,** posterior notch; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbg,** subintestinal ganglion; **spg,** supraintestinal ganglion; **sr,** receptaculum seminis; **vg,** visceral ganglion.

the hermaphroditic duct, at the side of which branches the single receptaculum seminis. The large mucous gland has one lobe above the albumen gland, and the free end bends. The large, rounded bursa copulatrix is situated at the end of the elongate, folded duct. There is a single secondary bursa copulatrix.

Discussion: *Philine puka*, *P. babai* (Valdés, 2008), and *P. habei* (Valdés, 2008) are the only members of the *P. aperta* clade that have been found at depths of at least 200 m.

Philine puka and P. habei (Valdés, 2008) are the only two species that have large pores on their gizzard plates, but these two species differ in the shape of their penial papillae and the dentition of the inner lateral teeth. The hammer-shaped papilla in *P. puka* is narrow with markedly unequal lobes and a reduced base. In *P. habei*, however, the lobes of the hammer-shaped papilla are almost equal in size, and the base is well developed. The inner lateral teeth of *P. habei* lack denticles, whereas those of *P. puka* have 39–44 small denticles.

Philine quadripartita Ascanius, 1772

(Figures 1F, 34, 35)

Philine quadripartita Ascanius, 1772:329, pl. 10, figs. a, b.

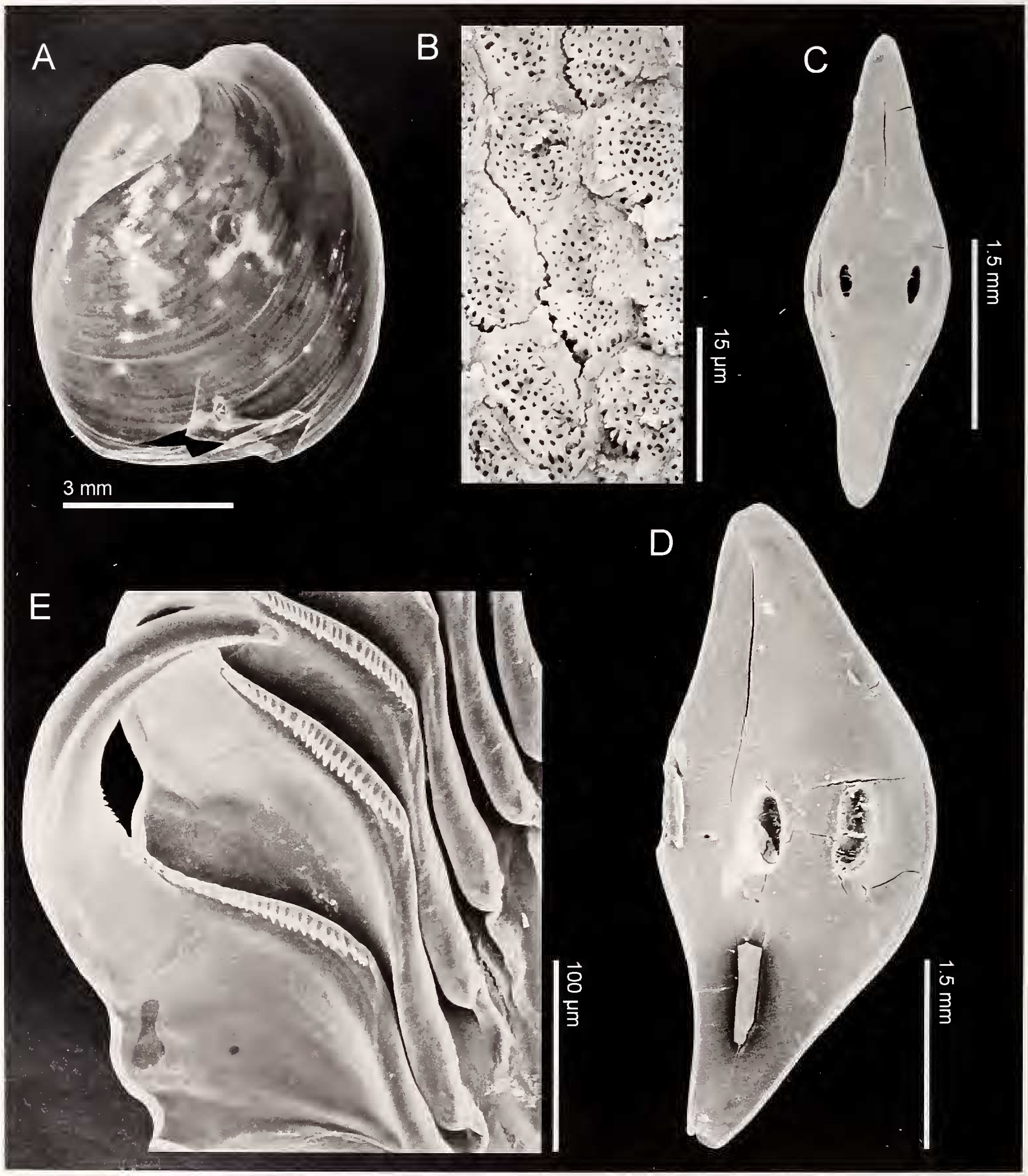

Figure 33. *Philine puka* (CASIZ 082128), photographs of internal hard structures: **A,** light photograph of a ventral view of the shell; **B,** gizzard-plate microstructure; **C,** SEM photograph of the unpaired gizzard plate; **D,** SEM photograph of a paired gizzard plate; **E,** SEM photograph of the radular teeth.

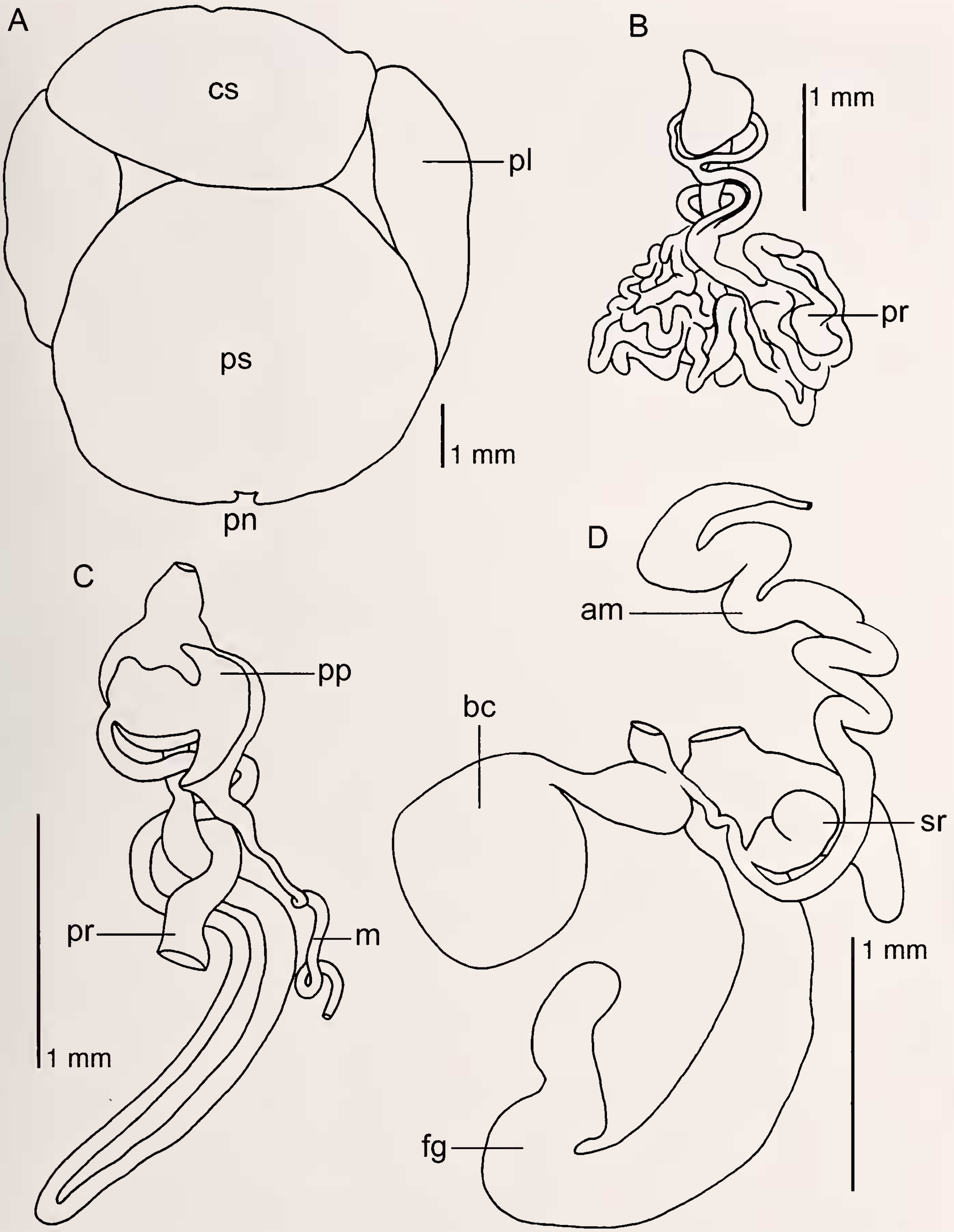

Figure 34. *Philine quadripartita* (CASIZ 066972), anatomy: **A,** dorsal view of a preserved animal; **B,** male reproductive system; **C,** penis and detail of the distal portion of the male reproductive system; **D,** female reproductive system. Abbreviations: **am,** ampulla; **bc,** bursa copulatrix; **cs,** cephalic shield; **fg,** female glands; **m,** muscle; **pl,** parapodial lobe; **pn,** posterior notch; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sr,** receptaculum seminis.

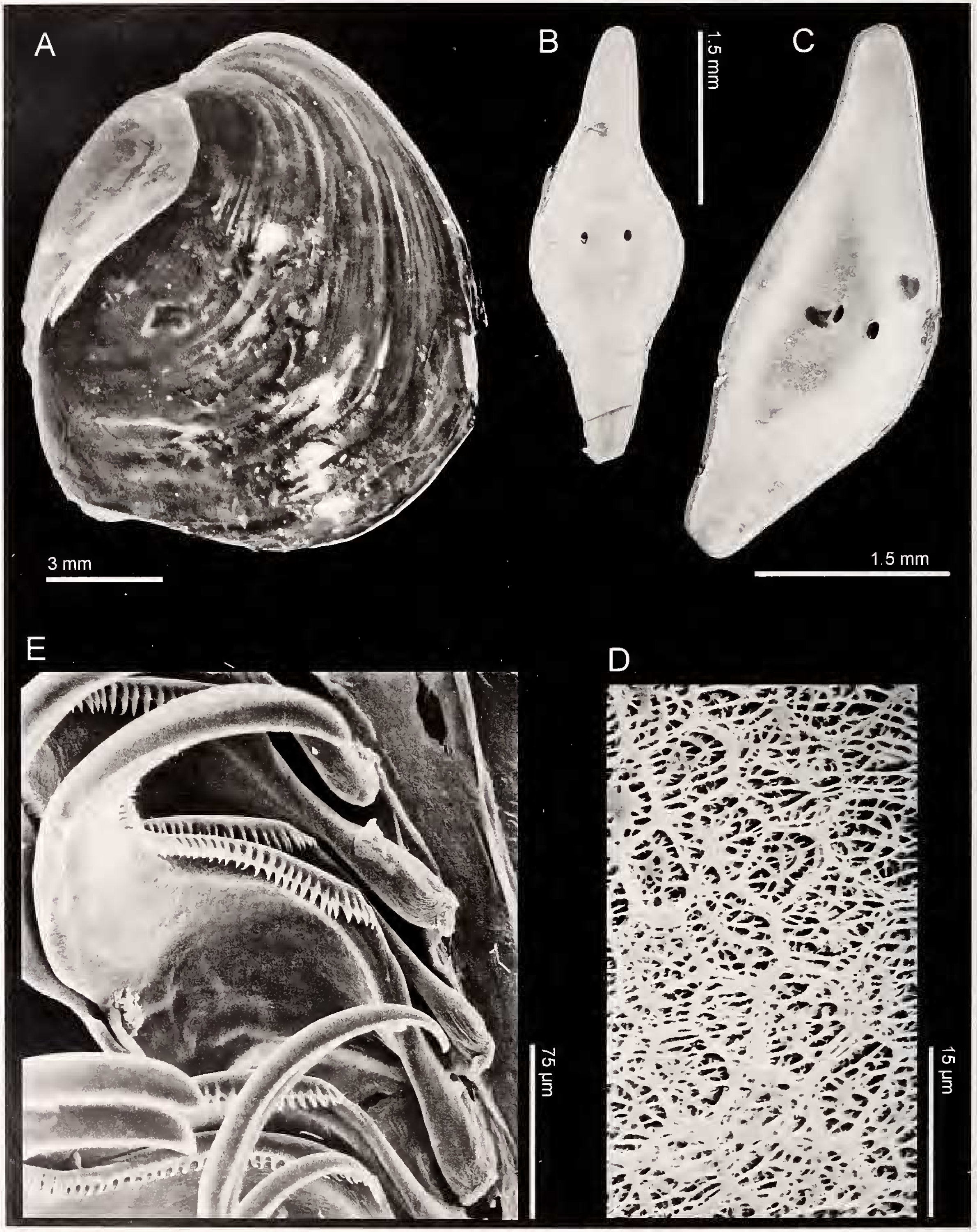

Figure 35. *Philine quadripartita*, photographs of internal hard structures: **A,** light photograph of a ventral view of the shell (CASIZ 118894); **B–E,** SEM photographs internal hard structures (CASIZ 066972); **B,** unpaired gizzard plate; **C,** paired gizzard plate; **D,** gizzard-plate microstructure; **E,** radular teeth.

Lobaria quadriloba Müller, 1776:226.
Lobaria quadrilobata Gmelin, 1791:3143.
Lobaria planciana Lamarck, 1801:63.
Philine aperta var., *patula* Jeffreys, 1867:458.
Philine apertissima deFolin, 1893:147.
Philine milneedwardsi Locard, 1897:35, pl. 1, figs. 7–9.
Philine aperta (Linnaeus) Guiart, 1901:111, figs. 2, 3, 5, 17, 18, 19, 21, 23, 24, 37–42, 50–52, 58–62, 78, 82, 86–88, 99; Brown, 1934:179, figs. 1–38; Thompson, 1976:132, fig. 68, misidentifications.

Material: CASIZ 066972, one specimen, dissected, Naples, Tyrrhenian Sea, Italy, collected by F. M. MacFarland. CASIZ 99117, one specimen, 8 m depth, Cabo Trafalgar, Strait of Gibraltar, Spain, September 27, 1994, T. M. Gosliner. CASIZ 118894, one specimen, outer Swansea Bay, Swansea, Wales, United Kingdom, J. Ellis, March 15, 1993.

Distribution: Known from the British Isles (Thompson, 1976) and throughout the Mediterranean (Cervera et al., 2006).

External morphology: The living animal (Figure 2F) is white and ranges in size from approximately 1 to 3 cm. The cephalic shield is longer than the posterior one (Figure 34A). The parapodial lobes are thick and muscular, and the posterior notch is deep.

Internal morphology: The shell (Figure 35A) is open with an ovate perimeter. Punctate microsculpture is absent, and the surface of the shell is smooth.

There are two dorsal oral glands, and a single, short ventral oral gland. The buccal mass is small. The radular formula is 16–19 × 1.0.1, and the broad inner lateral teeth have between 43 and 52 denticles (Figure 35E). The crop is indistinct and, although the gizzard is muscularized, muscles do not cover the three large gizzard plates. The gizzard plates are spindle-shaped with two medium-sized pores (Figure 35B, C). The unpaired plate (Figure 35B) is smaller than the other two. The microsculpture (Figure 35D) consists of regularly arranged polygons. The structure within each polygon is disorganized. The salivary glands are short.

The supraintestinal ganglion is adjacent to the fused pleural-parietal ganglion. The osphradial nerve branches off from halfway between the supraintestinal ganglion and the visceral ganglion. The genital ganglion is fused to the visceral one, which is, in turn, fused to the subintestinal ganglion.

The penial sac is ovate, and the penial papilla is hammer-shaped (Figure 34B, C). The hammer handle is a simple stalk. The lobes of the hammer head are subequal. One lobe protrudes over the prostate, stretching the shape of the penial sac. The prostate branches to the ejaculatory duct, and the posterior end is connected to the penial sac by a long muscle. The prostate is composed of a distinct aggregation of glandular cells. The ejaculatory duct is short and surrounded by much of the prostate.

The convoluted ampulla narrows (Figure 34D) into the hermaphroditic duct, at the side of which branches a single, long, and narrow receptaculum seminis. The bursa copulatrix is large with a short, thick stalk, and there is a single secondary bursa copulatrix.

Discussion: *Philine quadripartita* is the most extensively studied species in this genus, and there are detailed descriptions of the anatomy and developmental biology (Brown, 1934) and diet (Hurst, 1965), perhaps because its distribution includes the Mediterranean and the British Isles, areas in which the fauna is well known. However, most subsequent authors followed the convention of Lemche and others and considered their material to be *P. aperta*.

Philine quadripartita and *P. aperta* are very similar in their morphology, and they have often been considered synonymous. However, we found consistent differences that justify separating the two species. First, the gizzard plates of *P. quadripartita* are proportionately smaller and narrower, whereas the paired plates of *P. aperta* are broad, even approximating circularity in one drawing by Marcus & Marcus (1966:fig. 9). Second, the gizzard-plate microsculpture of the two species is different. In *P. quadripartita*, the microsculpture consists of flat polygons within which there is no obvious pattern. In *P. aperta*, however, the polygons are indented, more circular, and contain a regular subsculpture. Third, the penial papilla in *P. quadripartita* is smaller, and the knob on the penial stalk is less pronounced. Fourth, the penial papilla of *P. quadripartita* extends in a pointed extension of the penial sack, whereas in *P. aperta* the entire papilla is contained in a rounded sac. Finally, the egg mass is globular in *P. quadripartita* (Guiart, 1901:fig. 16; Rudman, 1998c) and elongate and tubular in *P. aperta* (Figure 2B).

Philine sarcophaga Price, Gosliner, and Valdés, sp. nov.

(Figures 36, 37)

Type material: Holotype: SAM, Meiring Naude Cruise, Station SM 67, specimen 22 mm, coarse sand, 680–700 m depth, 27°14.8′S, 32°54.6′E, May 20, 1976. Paratypes, CASIZ 175006, Meiring Naude Cruise, Station SM 67, two specimens, 15–18 mm, one dissected, coarse sand, 680–700 m depth, 27°14.8′S, 32°54.6′E, May 20, 1976.

Distribution: Known only from the tropical Kwazulu Natal coast of South Africa.

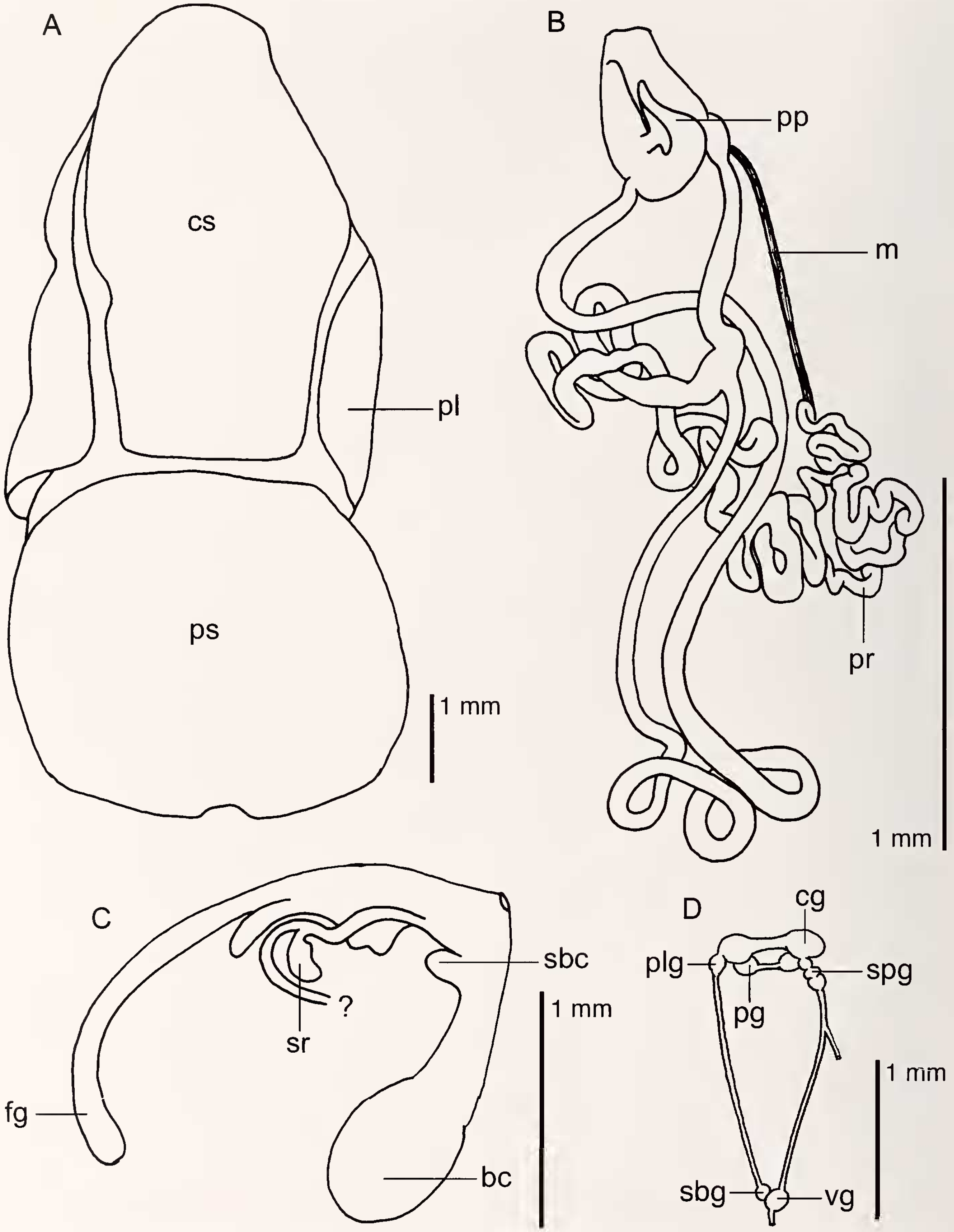

Figure 36. *Philine sarcophaga* (CASIZ 175006), anatomy: **A,** dorsal view of a preserved animal; **B,** male reproductive system; **C,** female reproductive system; **D,** nervous system. Abbreviations: **bc,** bursa copulatrix; **cg,** cephalic ganglion; **cs,** cephalic shield; **fg,** female glands; **m,** muscle; **pg,** pedal ganglion; **pl,** parapodial lobe; **plg,** parietal-pleural ganglion; **pp,** penial papilla; **pr,** prostate; **ps,** posterior shield; **sbc,** secondary bursa copulatrix; **sbg,** subintestinal ganglion; **spg,** supraintestinal ganglion; **sr,** receptaculum seminis; **vg,** visceral ganglion.

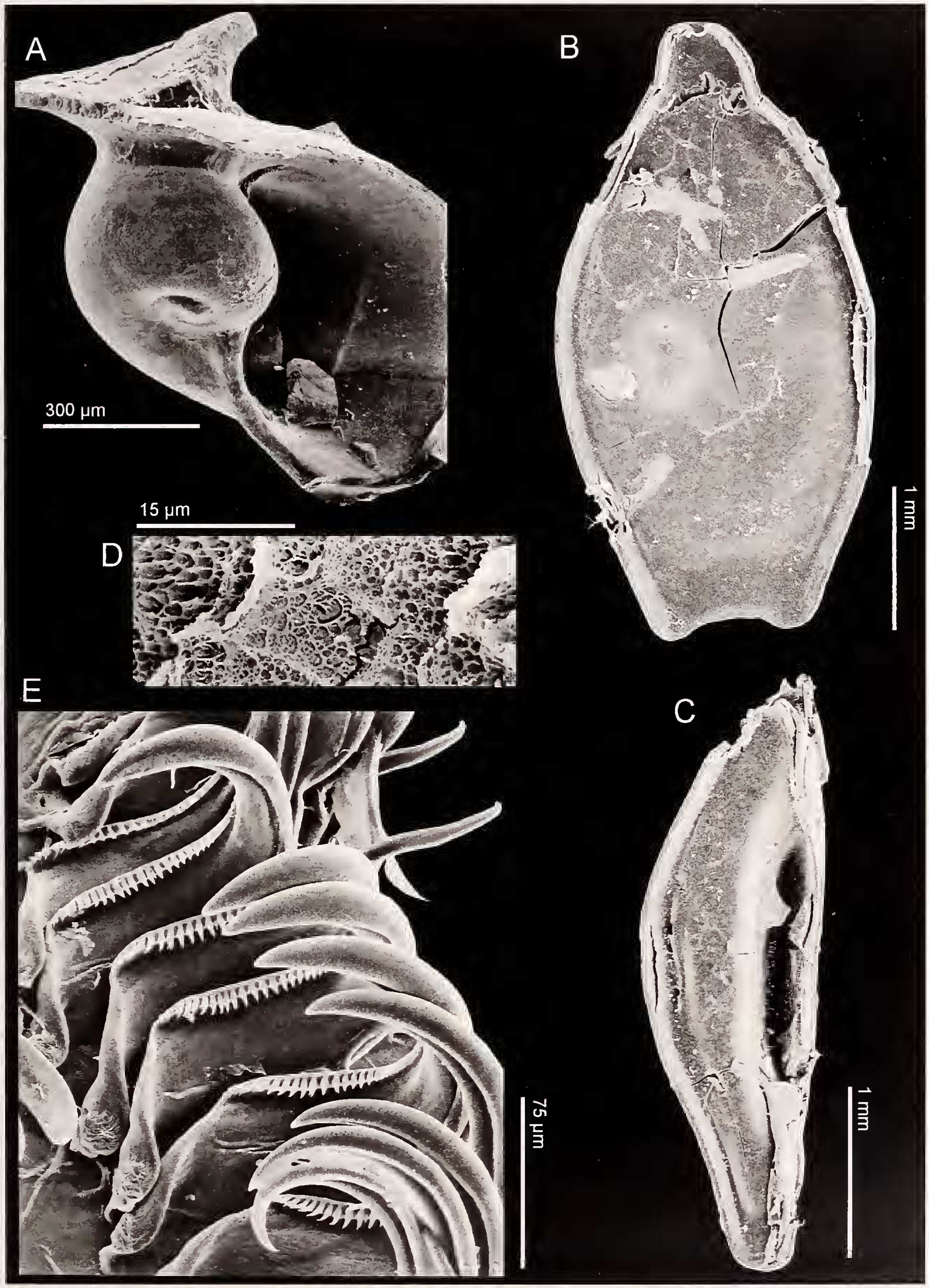

Figure 37. *Philine sarcophaga* (CASIZ 175006), SEM photographs of internal hard structures: **A,** protoconch; **B,** unpaired gizzard plate; **C,** paired gizzard plate; **D,** gizzard-plate microsculpture; **E,** radular teeth.

Etymology: The specific epithet, *sarcophaga*, refers to the coffin-shaped, unpaired gizzard plate.

Type locality: Kwazulu Natal, South Africa.

External morphology: The preserved specimens are white and vary in size from approximately 10 to 12 mm. The cephalic shield is longer than the posterior one (Figure 36A). The parapodial lobes are thin, and the posterior notch is shallow.

Internal morphology: The punctate shell (Figure 37A) is relatively tightly coiled for a *Philine*.

There are two dorsal oral glands and one ventral oral gland. The buccal bulb is reduced, and the radular formula is 18–19 × 1.1.0.1.1 (Figure 37E). The inner lateral teeth are broad with 18–31 small denticles. The outer laterals are thin and elongate, without denticles. The gizzard is muscularized and covers the two smaller plates but not the larger unpaired plate. The gizzard lacks a distinct crop posterior to the plates. The two paired plates are spindle-shaped with long slits on the flatter side (Figure 37C). The unpaired plate is much larger than the others and more rhomboidal (Figure 37B); its anterior end is rounded, and its posterior end is concave; it lacks slits, and it is larger than the other two plates. The plate microsculpture (Figure 37D) consists of a meshwork of polygons. The salivary glands are short.

The nervous system (Figure 36D) is euthyneurous. The fused pleural-parietal ganglion is adjacent to the anterior supraintestinal ganglion. The visceral ganglion is fused to the subintestinal ganglion. It is not known whether the genital ganglion is fused to the visceral ganglion.

The penial papilla (Figure 36B) is hammer-shaped, and the lobes of the hammer head are markedly unequal. The papilla rests in the penial sac. The elongated prostate branches to the ejaculatory duct, which is long and not covered by the prostate.

The ampulla (Figure 36C) narrows into the hermaphroditic duct, at the side of which branches the single receptaculum seminis. The large mucous gland has one lobe but may might be fully mature. The bursa copulatrix is large and rounded with a thick, elongate duct. There is one secondary bursa copulatrix.

Discussion: The paired gizzard plates are similar to those in *P. infundibulum*, in that they are flat on one edge and curved on the other edge. The plates in *P. sarcophaga* have two slits, with the slit along the long edge being much larger than the other. However, *P. infundibulum* has only one slit, which may be homologous to the larger slit in *P. sarcophaga*. The unpaired plates in both species are symmetrical, although, in *P. sarcophaga*, the anterior end is rounded and extended and the posterior end is concave, whereas in *P. infundibulum* both ends are simply rounded.

The penial papilla of *P. sarcophaga* is quite different from that of *P. infundibulum*. Instead, it is more similar to that of *P. orientalis*. The hammer-shaped tip of the papilla is small with markedly subequal lobes, but it is appressed with a fat base, and an additional large lobe swings up and around from the base, terminating in a point.

Another species described from South Africa is *Philine berghi* Smith, 1910. This species originally was misidentified as *P. capensis* by Bergh (1907). *Philine capensis* Bergh, 1907, was shown to be a junior homonym of *B. capensis*, which has been shown to be a junior synonym of *P. aperta* (Smith, 1910). Based on this fact, Smith erected a new name, *P. berghi*, for the species described in Bergh's article. O'Donoghue (1929) also referred to *P. berghi*. As in *P. sarcophaga*, *P. berghi* has a large rhomboidal gizzard plate without pores (Bergh, 1907:pl. 5, fig. 15), but *P. berghi* has two rows of outer lateral teeth, as opposed to the single row found in *P. sarcophaga*. In addition, the medial plate of *P. berghi* is somewhat smaller than the two lateral plates (described but not illustrated by Bergh), whereas in *P. sarcophaga* the medial (unpaired) plate is much larger that the lateral plates. No additional material matching Bergh's description has been found in any of the material housed in the collections of the South African Museum. Further distinctions must await the discovery of additional material matching Bergh's description.

Philine thurmanni thurmanni Marcus and Marcus 1969

Philine thurmanni thurmanni Marcus and Marcus, 1969:14–17, figs. 23–28.

Distribution: South Atlantic Ocean off the coast of Argentina.

External morphology: The living animal is white and varies between 2 and 9.5 mm. The cephalic shield is shorter than the posterior shield.

Internal morphology: The shell, which has prominent punctate sculpture, is ovate and only slightly coiled.

The buccal bulb is reduced, and the radula has formula 14–16 × 1.1.0.1.1. The inner lateral teeth are broad with an unspecified number of small denticles. The gizzard is muscularized and surrounded by three large, equal-sized plates. The plates lack any pores or slits. The gizzard lacks a distinct crop.

The penial papilla is hammer-shaped, and the lobes of the hammer head are markedly unequal. The papilla rests in the penial sac. The elongated prostate branches to the ejaculatory duct.

Discussion: The summary above is based on the original description in Marcus & Marcus (1969) and Marcus (1974). These descriptions are sufficiently complete to identify the species in the *aperta* complex, so we did not deem it necessary to analyze additional material. Because Marcus & Marcus (1969) and Marcus (1974) did not describe the nervous system or female reproductive anatomy, many of the character states for this species are missing from our matrix. Still, the branched ejaculatory duct, the hammer-shaped penial papilla, and the spindle-shaped gizzard plates place this species within the *P. aperta* clade.

PHYLOGENETIC ANALYSIS

Despite the description of more than 100 species of *Philine* and the erection of many different genera (including *Hermania* Monterosato, 1884; *Laona* A. Adams, 1865; *Philinorbis* Habe, 1950; *Yokoyamaia* Habe, 1950; *Globophiline* Habe, 1958; and *Spiniphiline* Gosliner, 1988), no study has been undertaken to construct a phylogenetic hypothesis of the group or to test the monophyly of any of these genera. We present an initial phylogeny of *Philine* species, including two outgroup taxa and 26 ingroup taxa that span much of the variability of the genus based on the analysis of 46 morphological characters.

Morphological Variability and Character Polarity

We have included 46 characters to determine phylogenetic relationships within the genus. Polarity was determined by using *C. alba* and *S. mundus*, two presumed close relatives of *Philine*, as outgroups. Twenty-six ingroup taxa were included in the analysis. Character polarities were determined using outgroup comparison in the phylogenetic analysis. The character matrix is presented in Table 2. All multistate characters are treated as unordered. The following characters and states were used.

Body

1. **Animal color:** The outgroup species and most *Philine* species are uniformly white in their body color. The known exceptions are *Philine caledonica* Risbec, 1951; *Philine rubra* Bergh, 1905; *Philine rubrata* Gosliner, 1988 (fig. 2H), and *Philine orca* Gosliner, 1988 (fig. 2G). 0: white; 1: not white.
2. **Ratio of cephalic shield to posterior shield:** Both in *Cylichna* and *Scaphander*, the cephalic shield is shorter than the posterior shield. This arrangement is plesiomorphic in *Philine*, but some species have cephalic shields that are the same length as the posterior shield, and others have cephalic shields that are even longer than the length of the posterior shield. This character is difficult to code in animals that were not relaxed before being preserved, because the manner in which the mantle contracts dictates body shape. In all cases, this character was determined from photographs of living animals or from preserved specimens that are well extended. 0, short cephalic shield; 1, long cephalic shield; 2, cephalic and posterior shields equal.
3. **Parapodial lobes:** Parapodial lobes span the sides of the cephalic shield. They are plesiomorphically weak and flimsy, but they can be muscular, as in *P. aperta*, *P. orientalis*, and *P. quadripartita*. 0, narrow; 1, thick.
4. **Posterior notch:** The posterior end of the posterior shield can be rounded or notched. A notch, even if actually present, is not always evident in all preserved specimens. Thus, it was necessary to examine multiple specimens to code this character effectively. In species, such as *P. aperta* and *P. sarcophaga*, the posterior notch is shallow. In species such as *P. auriformis*, the posterior notch is deep. 0, absent; 1, shallow; 2, deep.
5. **Elongate skirt:** In *Philine pruinosa* and *P. rubrata*, an elongate skirt wraps around the posterior shield and opens at the posterior end. This character is illustrated elsewhere (Gosliner, 1988:fig. 4). It applies only to species with a robust mantle that covers the shell, and thus cannot be coded for *Philine lima* and *P. t. thurmanni*, whose shells are covered by only a thin membrane. 0, absent; 1, present.
6. **Mantle cavity:** The mantle cavity is located on the right side of *Scaphander* and *Cylichna*, but it is located at the posterior end of the animal in all *Philine* species. We used this character to distinguish the ingroup from the outgroup. 0, right; 1, posterior.

Shell

7. **Shell:** *Scaphander mundus* and *C. alba* have external shells, whereas all *Philine* species have internal shells. This character differentiates *Scaphander* and *Cylichna* from the ingroup. 0, external; 1, internal.
8. **Shell sculpture:** *Scaphander mundus* and the more basal members of *Philine* have punctate shells. Other authors describe this punctation as "catenoid" (e.g., Lemche, 1948) or spiral sculpture (e.g., Marcus & Marcus, 1969). Our observations suggest that juveniles are usually punctate, but that, in some species, the adults deposit an additional, smooth layer over the punctations. Only adult shells were used to code this character. 0, punctate; 1, smooth.

Table 2
Character matrix of *Philine* and outgroups

	alba	*alboides*	*angasi*	*aperta*	*auriformis*	*babai*	*berghi*	*elegans*	*falklandica*	*fenestra*	*finmarchica*	*gibba*	*habei*
1	0	0	0	0	0	0	?	0	0	0	0	0	0
2	1	0	1	1	1	2	?	2	0	1	2	0	1
3	0	0	0	1	0	0	?	0	0	0	0	0	0
4	0	0	0	1	2	0	?	2	1	0	1	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0
6	1	1	1	1	1	1	1	1	1	1	1	1	1
7	1	1	1	1	1	1	1	1	1	1	1	1	1
8	1	1	1	1	0	0	?	1	1	0	1	1	1
9	1	1	1	1	1	1	?	?	0	1	0	1	1
10	0	0	1	0	0	2	?	0	0	0	0	0	2
11	0	0	2	1	1	2	?	1	2	1	1	2	2
12	0	0	1	1	?	1	?	1	0	1	1	0	1
13	0	0	1	1	1	1	?	1	0	1	1	0	1
14	1	2	2	2	2	2	2	2	1	2	2	1	2
15	1	1	3	3	2	2	1	3	1	2	3	1	3
16	0	0	0	0	0	0	?	0	0	0	0	0	3
17	0	0	0	0	0	0	?	0	0	0	0	0	0
18	0	0	1	1	1	1	?	1	0	1	1	0	1
19	1	1	0	0	0	0	?	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	1	1	1	1	1	1	0	1	1	0	1
22	0	0	1	1	1	1	?	1	0	1	1	1	1
23	0	0	1	1	1	1	?	1	0	1	1	0	1
24	0	0	0	0	0	2	?	1	0	0	0	0	0
25	0	0	1	1	?	0	?	1	?	1	?	?	1
26	0	0	1	0	0	1	?	1	0	0	0	0	0
27	0	0	1	1	0	1	1	1	?	1	0	?	1
28	0	0	2	2	0	2	2	2	0	0	0	0	2
29	NA	NA	0	0	NA	1	?	1	?	0	NA	?	0
30	0	0	2	2	0	0	0	2	0	0	0	0	2
31	?	?	1	1	?	?	?	1	?	?	?	?	2
32	0	0	0	0	2	2	?	0	0	2	0	0	0
33	0	0	1	1	1	1	?	1	0	1	1	0	1
34	0	0	2	2	2	2	?	2	0	2	2	0	2
35	NA	NA	0	0	0	0	?	1	NA	1	0	NA	1
36	?	?	0	0	0	1	?	0	?	0	0	?	1
37	0	0	1	1	1	1	?	1	0	1	1	0	1
38	?	?	1	0	0	1	?	0	?	0	?	?	0
39	?	?	0	1	1	0	?	0	?	1	?	?	1
40	0	0	0	0	0	0	?	0	0	0	0	1	0
41	0	0	0	0	0	0	?	0	1	0	0	0	0
42	0	0	0	0	0	0	?	0	0	0	1	1	0
43	1	1	1	1	1	1	?	1	0	2	0	0	1
44	1	1	1	1	1	1	1	1	1	1	1	1	1
45	0	0	2	2	2	2	?	2	0	2	2	1	2
46	1	1	1	1	1	1	?	1	1	?	1	0	1

The character states are indicated with numbers, 0: plesiomorphic condition, 1–2: apomorphic conditions. Question marks indicate unknown data. NA indicates non-applicable characters.

9. **Shell coiling:** The shells of *Scaphander* and *Cylichna* are more tightly coiled (i.e., their shells have more whorls or a lower expansion rate) than the shells in most *Philine* spp., Thus, *Philine* shells have a higher whorl expansion rate (following the terminology in Raup, 1961). A high whorl expansion rate means that the posterior shield is broad and disc-shaped. 0, tightly coiled; 1, high whorl expansion rate.

Digestive System

10. **Ventral oral glands:** The number of ventral oral glands in *Philine* varies between one and two. We

Table 2
Extended

infundibulum	*lima*	*orca*	*orientalis*	*paucipapillata*	*pruinosa*	*puka*	*quadrata*	*quadripartita*	*rubrata*	*sarcophaga*	*thurmanni*	*Spiniphiline kensleyi*	*Cylichna alba*	*Scaphander mundus*
0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
1	1	0	1	1	2	2	2	1	0	1	0	1	0	0
0	0	0	1	1	0	0	0	1	0	0	?	0	0	0
?	0	1	0	2	2	2	1	2	2	1	?	2	0	0
0	?	0	0	0	1	0	0	0	1	0	?	0	?	?
1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
1	0	0	0	1	0	1	0	1	0	1	0	1	1	0
1	0	1	1	1	0	1	1	1	1	1	0	0	0	0
0	?	1	1	1	?	0	?	0	0	0	?	1	?	?
1	?	1	2	1	?	1	?	1	1	1	?	0	?	?
1	?	1	1	1	?	1	0	1	1	1	?	1	0	0
1	1	1	1	1	?	1	1	1	1	1	?	0	0	0
2	2	2	2	2	2	2	2	2	2	2	2	2	0	1
2	1	1	3	3	0	3	1	3	1	2	2	2	0	3
0	3	2	0	0	0	0	0	0	1	0	0	0	0	0
0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
1	0	0	1	1	?	1	1	1	0	1	1	0	0	0
0	1	1	0	0	?	0	?	0	0	0	0	0	0	0
0	1	1	0	0	1	0	1	0	2	0	0	0	0	0
1	NA	NA	NA	NA	NA	NA	NA	1	NA	1	?	1	0	2
1	NA	NA	NA	NA	NA	NA	NA	1	NA	1	?	1	0	0
1	NA	NA	NA	NA	NA	NA	NA	1	NA	1	1	1	0	1
0	NA	NA	NA	NA	NA	NA	NA	0	NA	0	0	0	0	0
0	NA	NA	NA	NA	NA	NA	NA	1	NA	1	?	?	?	?
0	NA	NA	NA	NA	NA	NA	NA	0	NA	0	0	0	0	0
1	NA	NA	NA	NA	NA	NA	NA	1	NA	1	0	1	0	0
1	NA	NA	NA	NA	NA	NA	NA	2	NA	1	0	2	0	2
1	NA	NA	NA	NA	NA	NA	NA	0	NA	1	NA	?	NA	NA
0	NA	NA	NA	NA	NA	NA	NA	2	NA	0	0	0	0	0
?	NA	NA	NA	NA	NA	NA	NA	1	NA	?	?	?	?	?
1	NA	NA	NA	NA	NA	NA	NA	0	NA	2	0	0	0	0
1	0	0	1	1	?	1	0	1	0	1	1	0	0	0
2	3	0	2	2	?	2	0	2	0	2	2	0	0	0
0	NA	NA	0	1	NA	1	NA	0	NA	1	1	NA	NA	NA
0	?	?	0	0	?	1	?	1	?	0	0	?	?	?
1	0	0	1	1	?	1	0	1	0	1	1	0	0	0
1	?	?	1	0	?	0	?	0	?	1	?	?	?	?
1	?	?	0	1	?	1	?	1	?	0	?	?	?	?
0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
0	0	1	0	0	?	0	0	0	0	0	0	0	0	0
0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
1	0	0	1	1	?	1	0	1	0	1	?	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
2	1	2	2	2	?	2	1	2	2	2	?	2	1	0
1	0	1	1	1	?	1	0	1	1	1	?	1	1	1

do not know how many ventral oral glands *C. alba* and *S. mundus* have. 0, one; 1, two; 2, absent.

11. **Dorsal oral glands:** *Philine* species have zero, one, or two dorsal oral glands. We do not know how many dorsal oral glands *C. alba* and *S. mundus* have. 0, one; 1, two; 2, zero.
12. **Salivary glands:** The salivary glands may be longer than the buccal mass, as in *P. alba* and *P. alboides*, or they may be short and stubby, as in the members of the *P. aperta* clade, where they are much shorter than the buccal mass. 0, long; 1, short.
13. **Size of radula relative to body:** The outgroup taxa and the basal members of *Philine* have a larger radula than the species of the *Philine aperta* clade. 0, large; 1, reduced.
14. **Rachidian tooth:** The rachidian tooth is only present in the outgroup and in such basal members of *Philine* as *Philine gibba* and *Philine falklandica.*

It may be vestigial or absent in *P. alba*. When present in *Philine*, the rachidian tooth is small and may be vestigial. 0, large; 1, small; 2, absent.

15. **Number of outer lateral teeth:** *Cylichna alba* and *S. mundus* have many lateral teeth, as does *P. pruinosa* (Thompson, 1976). As shown by Gosliner (1994:279), opisthobranch outer teeth are not homologous with the marginal teeth found in Vetigastropoda and are therefore referred to as outer lateral rather than marginal teeth. Some basal members of *Philine* have two outer lateral teeth. Within the *P. aperta* clade, species have either one outer lateral (e.g., *P. sarcophaga*) or none (e.g., *P. orientalis*). 0, many teeth; 1, two teeth; 2, one tooth; 3, no teeth.
16. **Inner lateral denticles:** Although inner lateral denticles are absent in *P. lima* (Lemche, 1948) and *P. habei* (Valdés, 2008), most species have 30–80 minute denticles. *Philine rubrata* is autapomorphic for having 10–11 elongate denticles, and *P. orca* is autapomorphic for one large denticle (Gosliner, 1988). 0, several small; 1, some medium; 2, one large; 3, absent.
17. **Width of inner lateral ridge:** Most inner lateral teeth have a broad ridge on which the denticles are located, whereas *P. lima* and *P. pruinosa* have a narrow ridge. 0, broad; 1, narrow.
18. **Crop:** Some species have a distinct crop above the gizzard, whereas others lack the crop entirely. *Philine infundibulum* has a widening of the esophagus below the gizzard, but this area does not seem to be homologous with the crop as it has a different structure. 0, distinct; 1, indistinct.
19. **Muscularized gizzard:** *Philine alba* and *P. alboides* have virtually no muscularization of the gizzard and are therefore similar to the Aglajidae. All other *Philine* that have a gizzard that is muscularized. 0. muscularized; 1, not muscularized.
20. **Plates present:** The plesiomorphic condition for *Philine* is to have three prominent gizzard plates, as in the outgroup taxa. Some species, such as *P. rubrata* (Gosliner, 1988), have plates that are reduced to chitinous ridges within a muscular region of the esophagus and are considered vestigial, and some species have no plates at all. Some authors have observed reduced plates in *P. quadrata*, but others claims that *P. quadrata* lacks plates entirely (Thompson, 1976; present study). We infer that, when *P. quadrata* plates are present, they must be vestigial. 0, three plates present; 1, vestigial; 2, absent.
21. **Shape of gizzard plates:** *Cylichna*, *Scaphander*, and some *Philine* species have gizzard plates that look like kidney beans. *Scaphander* has similarly shaped plates, but they are tiered so that a notch between the layers is visible in profile. Members of the *P. aperta* clade have spindle-shaped plates. The spindle may be somewhat triangular. 0, kidney-bean shaped; 1, spindle-shaped; 2: tiered.
22. **Esophagus goes through plates:** In some species, the gizzard lacks definition within the plates and no distinct esophageal duct is observed within the gizzard. In other species, the esophagus is clearly present as a distinct tube that passes through the gizzard. 0, without definition; 1, distinct tube.
23. **Plate size relative to body size:** Some *Philine* species have small plates, whereas others have large ones. This refers to species that have three plates in character 20, and it refers to the size of these plates. 0, small; 1, large.
24. **Plate margin:** Most *Philine* species have plates with a smooth margin. *Philine elegans* is autapomorphic for a fringed plate, and *P. babai* (Valdés, 2008) is autapomorphic for irregular crenulations. 0, smooth; 1, fringed; 2, irregular.
25. **Texture in plate microstructure:** Fine microstructure of the exterior (rather than esophageal) side of the plates arranged as a series of irregularly shaped polygons may be apparent when the gizzard plates are observed under SEM at the micrometer scale. Both outgroup taxa lack microsculpture. 0, absent; 1, present.
26. **Twisted plates:** The paired plates in *P. angasi*, *P. elegans*, and *P. babai* Valdés, 2008, have an S-like twist along the long axis. 0, absent; 1, present.
27. **Two plates that are paired:** Some *Philine* species have equal-sized plates, as does *Cylichna*. In other species, however, there are two paired plates that are mirror images of each other 0, paired plates absent; 1, paired plates present.
28. **Sizes of unpaired plates:** *Philine* species can have two paired plates of the same size, an unpaired plate that is smaller than the paired plates, or an unpaired plate that is larger than the paired plates. 0, equal; 1, unpaired plate is larger; 2, unpaired plate is smaller.
29. **Shapes of unpaired plates:** When one of the gizzard plates differs from the other two plates, it may be spindle-shaped, as in *P. aperta*, or rhomboidal, as in *P. elegans*. This character describes the shape of the unpaired plate, and it is therefore not applicable to any taxa that do not have paired plates. 0, spindle; 1, rhomboidal.
30. **Plate pores:** Some of the gizzard plates have pores on their outer surface. 0, pores absent; 1, pores present.
31. **Pore size:** Pores on the gizzard plate can be small (*P. paucipapillata*; Figure 31B, C), medium (*P. aperta*; Figure 3A, B), or large (*P. puka*; Figure 33C, D). 0, small; 1, medium; 2, large.
32. **Slits on paired plates:** *Philine infundibulum* has one long slit on each of its paired plates. *P. babai*

(Valdés, 2008) and *P. sarcophaga* have two long slits on their paired plates. *Philine auriformis* and *P. fenestra* also have two long slits, but these slits are present on all three, equal-sized gizzard plates. 0, absent; 1, one long slit; 2, two long slits.

Reproductive System

33. **Relative length of the prostate:** Several members of *Philine* are characterized by a long and convoluted prostate that often extends beyond the length of the gizzard *in situ*, whereas other members have a short, simple prostate. 0, short and straight; 1, convoluted and elongate.
34. **Shape of penial papilla:** The penial papilla may be a simple cone, a bilobed point, or hammer-shaped. Sometimes the papilla is completely absent, as in *P. lima* (Lemche, 1948; Marcus & Marcus, 1969). 0, simple conical; 1, bilobed; 2, hammer; 3, absent.
35. **Hammer head lobes:** When the penial papilla is hammer-shaped, the lobes on the hammer "head" may be approximately the same size, or one lobe may be much larger than the other. 0, subequal; 1, markedly unequal.
36. **Penial papilla sac:** The base of a hammer-shaped penial papilla may fit within the penial sac or it may distend the sac. This character does not seem to vary within species and is therefore not likely a preservational artifact. 0, contained within sac; 1, distends the sac.
37. **Ejaculatory duct is a specialized branch of the prostate:** The ejaculatory duct may form a separate branch of the convoluted and elongate prostate. 0, absent; 1, present.
38. **Length of the ejaculatory duct:** The ejaculatory duct may be long, extending far below the prostate, as in *P. orientalis* (Figure 26B), or it may be short, as in *P. aperta* (Figure 3C). 0, short; 1, extends far beyond prostate.
39. **Ejaculatory duct surrounded by prostate:** The ejaculatory duct may be surrounded by the rest of the prostate (*P. angasi*), or it may be adjacent to the prostate (*P. aperta*). 0, naked; 1, covered.
40. **Spermatic bulb:** The simple prostate in *P. gibba* terminates in a muscular bulb that presumably facilitates sperm transfer. 0, absent; 1, present.
41. **Prostate lobe:** Both *P. falklandica* and *P. orca* have a simple prostate with a secondary lobe. 0, absent; 1, present.
42. **Prostate texture:** In *P. finmarchica* and in *P. gibba*, the prostate is nodulose. All of the other species in our sample have smooth prostates. 0, smooth; 1, nodulose.
43. **Secondary bursa copulatrix:** Members of the *P. aperta* clade have a small bursa copulatrix posterior to the primary bursa copulatrix at the terminus of the female reproductive system. *Philine fenestra* has two appressed secondary bursa copulatrices. 0, zero; 1, one; 2, two.
44. **Gonopore:** The gonopore in all *Philine* species is located at the posterior. The character was used to separate the in-group from the out-group because the gonopore both in *Scaphander* and in *Cylichna* is located on the right. 0, right; 1, posterior.

Nervous System

45. **Supraintestinal ganglion:** In the outgroup taxa, the supraintestinal ganglion has a posterior location. As the nervous system becomes more concentrated (cephalized), the ganglion migrates anteriorly. In some species, the supraintestinal ganglion can be anterior or adjacent to the parietal ganglion, and, in other species, it is located half-way between the visceral and parietal ganglia. 0, posterior; 1, fused to pleural; 2, adjacent to or adjoining the fused pleural-parietal ganglion.
46. **Subintestinal ganglion:** In some taxa, the subintestinal ganglion is distinct from the visceral one. In the vast majority of species, the subintestinal ganglion is adjacent to the visceral one. 0, distinct; 1, fused to visceral ganglion.

Phylogeny of the Philinidae

In the resulting phylogeny (Figure 38), 54 most parsimonious trees were retrieved after 1000 repetitions of a heuristic search using random start trees with stepwise addition. The trees had a length of 133 steps, a consistency index of 0.481, and a retention index of 0.693. Whether *Scaphander* or *Cylichna* was used as a single outgroup or both were used together, a monophyletic Philinidae was obtained and the tree topology was identical. In the phylogeny, *P. falklandica* is the most basal taxon and is the sister to the rest of *Philine*. Immediately above this node is a trichotomy with *P. gibba*, the clade containing *P. alba* and *P. alboides* and a clade containing the remainder of *Philine*. Within this remainder of *Philine* is a clade containing *P. berghi* and *Spiniphiline kensleyi* and two other larger clades. The smaller of these clades contains *P. orca*, *P. quadrata*, *P. lima*, and *P. pruinosa*. The sister clade to this smaller clade is the large *P. aperta* clade containing 15 species. At and near the base of the *P. aperta* clade are two small clades with *P. finmarchica* and *P. thurmanni* as sister species followed by *P. infundibulum* and *P. sarcophaga* as sister species. These are followed by a grade of three species, *P. babai*, *P. fenestra*, and *P. auriformis*. The majority of species in the *P. aperta* clade are in the large clade of species that are characterized by having gizzard plates with paired

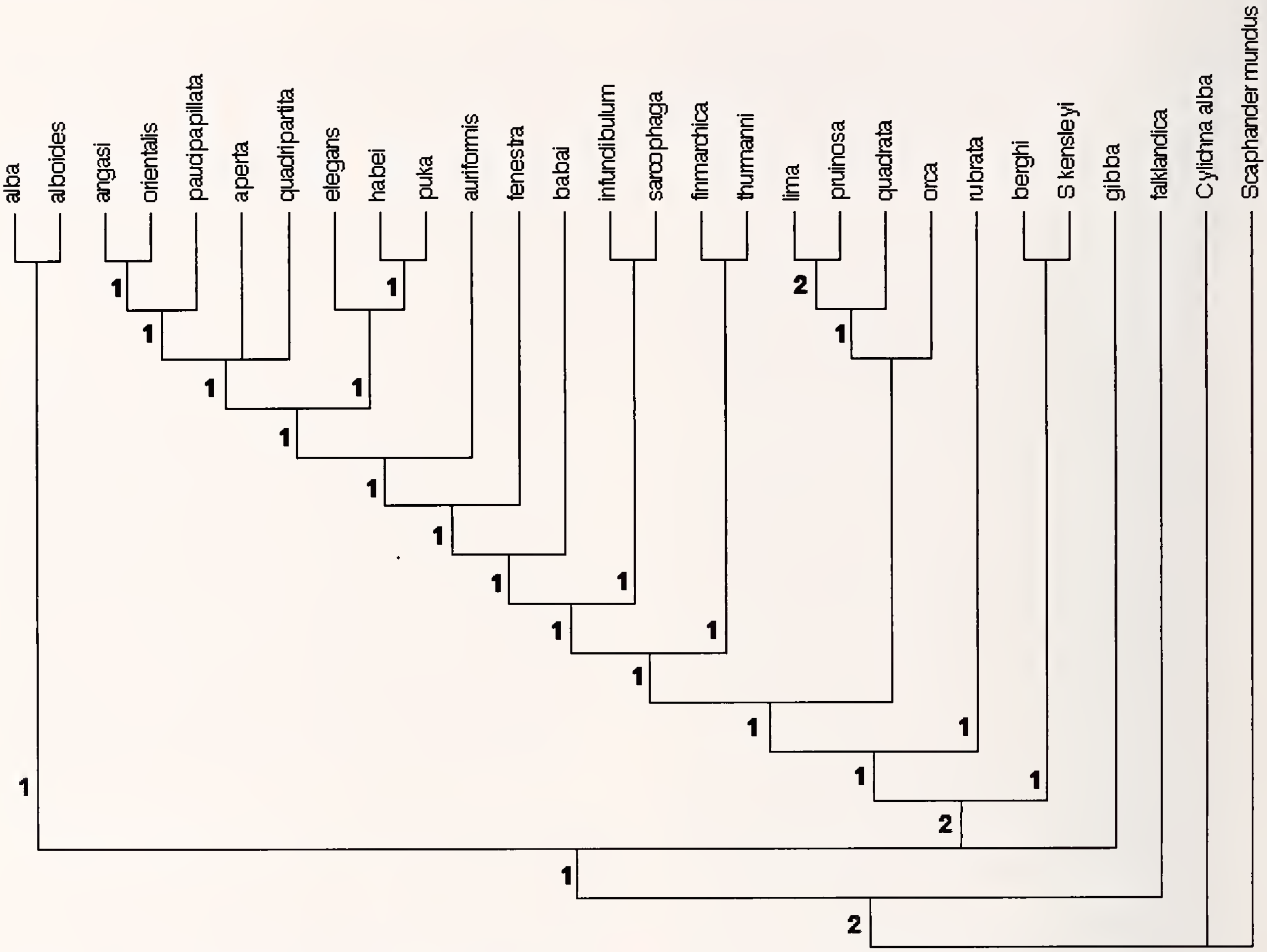

Figure 38. Strict consensus tree of *Philine* phylogeny showing Bremer support.

pores. These clades consist of two clades, the one that contains *P. elegans*, *P. habei*, and *P. puka* and a larger clade composed of *P. quadripartita*, *P. aperta*, *P. paucipapillata*, *P. orientalis*, and *P. angasi*.

A decay analysis of the resulting strict consensus (Figure 38) shows only moderate support for the resulting clades. Only three clades have a Bremer support value of 2, whereas each remaining clade has a value of 1. The clades with a support value of 2 are the clade of all *Philine*, the clade containing all members of *Philine* except *P. falklandica*, *P. gibba*, *P. alba*, and *P. alboides* (henceforth referred to as the derived-*Philine* clade), and the clade of *P. lima* and *P. pruinosa*. This fact strongly suggests that additional studies should be undertaken to investigate the phylogenetic relationships of *Philine*. Despite the low Brewer support, several nodes are supported by multiple characters (Figure 39). *Philine* is supported by four characters. The derived *Philine* clade is supported by eight synapomorphies. The *P. aperta* clade is supported by five synapomorphies. The clade containing the species with paired pores of the gizzard plates (the pored-*Philine* clade) is also supported by five synapomorphies.

Character Evolution

Several external morphological characters are oddly distributed in the resulting tree. For example, the relative length of the cephalic and posterior shields (character 2) is extremely variable, as is the presence or absence of a posterior notch (character 4). It is likely that these represent preservational artifacts rather than being representative of characters that exhibit little phylogenetic signal. It is imperative that external morphological characters be observed in living specimens whenever possible.

The resulting tree indicates that pigmented rather than white body color (character 1) evolved more than once in two distinct lineages. Again, additional documentation of color pattern in living specimens is necessary to obtain a better understanding of the evolution of pigmentation in *Philine*.

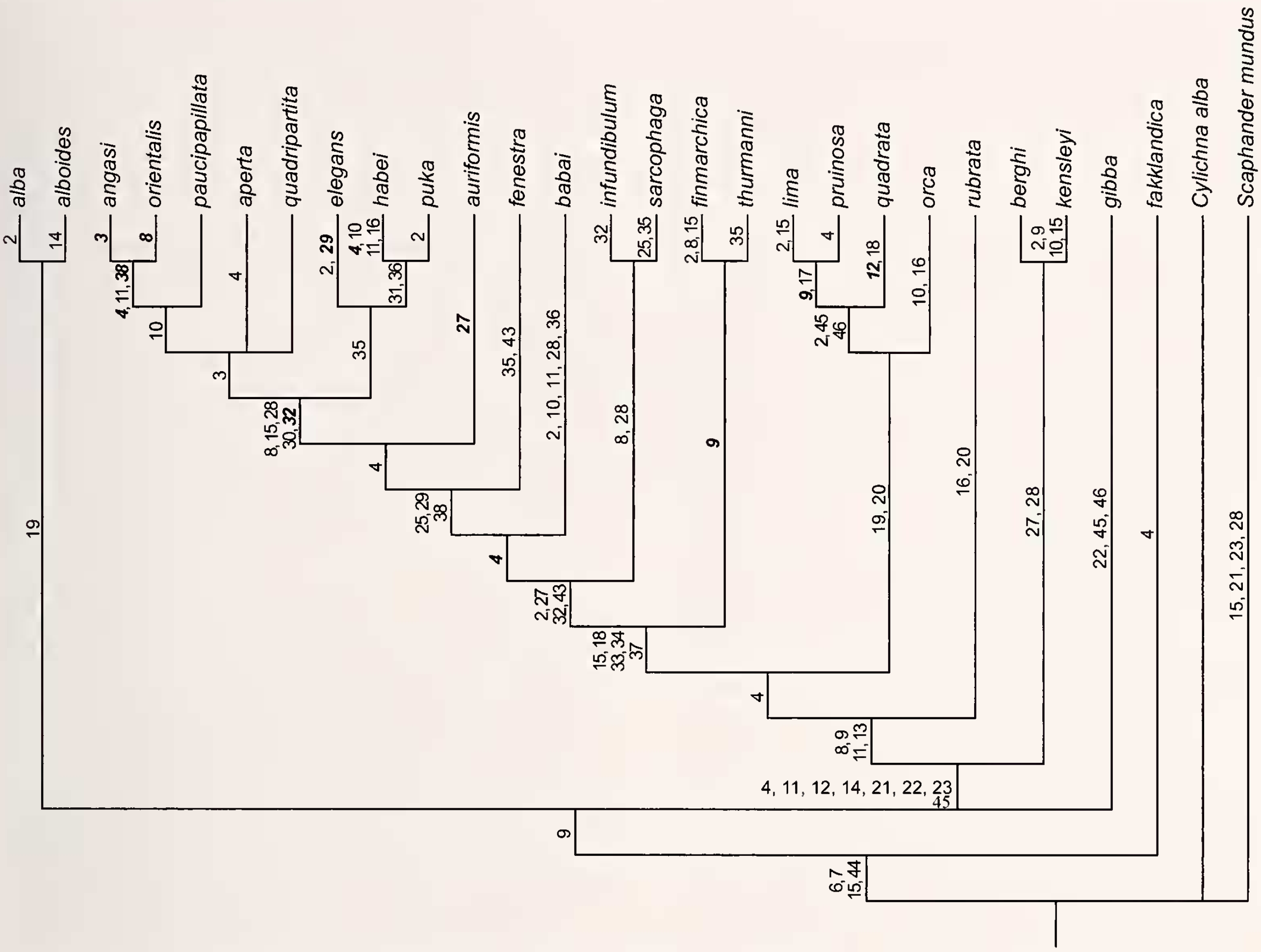

Figure 39. Strict consensus tree of *Philine* phylogeny showing character distribution. Characters in italics represent reversals.

The presence of thick parapodial lobes (character 3) is found only in the large shallow-water species of the pored-*Philine* clade (*P. orientalis*, *P. paucipapillata*, *P. aperta*, and *P. quadripartita*, but it seems to be absent in *P. angasi*).

It seems that most basal members of *Philine* have smooth shells without punctate sculpture (character 8). However, Gosliner (1994) argued that presence of punctate shell sculpture is plesiomorphic in opisthobranchs. Punctate sculpture is present in many of the moderately derived species of *Philine*. Although this might represent a reversal in these taxa, a more plausible scenario is that sculpture is not entirely lost in any *Philine* species but is present in postmetamorphic individuals. This scenario is supported by the fact that some postveliger shell regions of some specimens of *P. orientalis* have punctate sculpture, whereas other adult specimens entirely lack any evidence of such sculpture. It appears that subsequent shell calcification covered the layers that had bare sculpture. Well-developed sculpture seems to be present in adults of some species that attain a relatively small body size, further suggesting that sculpture may be ontogenetically linked to shells that are immediately postmetamorphic or in species that mature at a smaller body size and are probably pedomorphic. The same developmentally linked aspects also may be related with the apparent reversal of shell coiling patterns (character 9), which may be linked to pedomorphosis.

Characters 10 and 11, relating to the number of dorsal and ventral oral glands, indicate that derived conditions might have evolved independently or may represent a preservational artifact. These glands are often difficult to find in poorly preserved animals.

The presence of elongate salivary glands (character 12) characterizes the outgroup taxa and basal members of *Philine*. Elongate salivary glands are also present in the more derived *P. quadrata*.

A large radula relative to the size of the body (character 13) is characteristic of the outgroup and more basal *Philine* species. In more derived taxa, the size of the radula becomes reduced. Other radular features, such as loss of the rachidian tooth (character 14) and reduction in the number of lateral radular teeth (character 15) are found in more highly derived members of *Philine*. Presence of two outer laterals per side is characteristic of the *P. aperta* clade, with a further reduction to a single outer lateral per side in the pored-*Philine* clade.

The presence of a distinct crop (character 18) is found in the more basal members of *Philine*. Presence of an indistinct crop is another important synapomorphy of the *P. aperta* clade and is also found in *P. quadrata*.

The presence of spindle-shaped gizzard plates (character 21), as well as the presence of large plates (character 23), unites all taxa in the derived-*Philine* clade, as does the presence of an esophagus with a distinct tube (character 22). Other characters of gizzard-plate shape provide additional significant synapomorphies that unite larger clades. The clade that includes the subclade of *P. sarcophaga* and *P. infundibulum* and its sister group all have paired gizzard plates and one plate that is of a different size (character 27). This condition seems to have been reversed in *P. auriformis*, where all three plates are equal in size. In the pored-*Philine* clade, all taxa have an unpaired plate (character 28) that is smaller than the paired plates. This condition also unites *P. berghi* and *S. kensleyi*. In *P. sarcophaga* and *P. infundibulum*, the unpaired plate is larger than the paired ones. The presence of pores (character 30) unites the pored-*Philine* clade.

Several features of the reproductive system also provide important synapomorphies. Presence of an elongate, convoluted prostate gland (character 33), a hammer-shaped penial papilla (character 34), and presence of a separate ejaculatory duct (character 37) unite the *P. aperta* clade. The presence of a secondary bursa copulatrix (character 43) is synapormorphic for the clade that includes the subclade of *P. sarcophaga* and *P. infundibulum* and its sister group. Presence of a posteriorly situated gonopore (character 44) is synapomorphic for *Philine*.

It is evident that characteristics of radular morphology, the elaboration of the gizzard plates, the form of the penial complex, and the presence of exogenous sperm storage organs provide most of the characters that provide the structure of the tree presented. Most external morphological characters and characteristics of the nervous system appear to be less significant in shaping the phylogeny of *Philine*.

DISCUSSION

The majority of the species of *Philine* have been described strictly from the shell (see Pilsbry, 1895, for an example). There seems to be a great deal of convergence in shell morphology, and, as we reveal with our analysis of the *P. aperta* species complex, species with similar shells can have dramatically different anatomical features. Although conchological features may provide useful taxonomic characters in other clades—and perhaps even in other genera of Philinidae—more recent studies (Marcus & Marcus, 1966, 1969; Rudman, 1970, 1972b; Marcus, 1974; Gosliner, 1988) have demonstrated the necessity of describing detailed anatomical features to provide for definitive identification of species. Despite this fact, new species continue to be described from shells only (e.g., Linden, 1995). This creates great uncertainty as to the identity of species, and it makes it particularly difficult to reconcile conchological features with anatomical ones to produce an integrative taxonomy. Although the shell is important in identifying members of the genus *Philine* as it currently stands, it is not sufficient for determining the number of species within the groups, for deciphering relationships among the species, or for the identification of supraspecific taxa.

Our results indicate that the *P. aperta* species complex is a clade. Earlier systematists have synonymized many of the species in this clade, agreeing that all or most of the species that possess pores on their plates represent a single species or very few species. For example, in distinguishing between *P. aperta* and *P. orientalis*, Lemche (1948) cited Bergh (1901) as saying that "the number of species already established on [this] variation … is sufficiently large." What makes this quotation most amusing, perhaps, is that Lemche thought Bergh was synonymizing *P. aperta* and *P. quadripartita* rather than *P. aperta* and *P. orientalis*. This oversynonymization is surprising in that these taxa inhabit disparate biogeographical regions where the rest of the biota does not overlap. By including a breadth of anatomical characters, including (but not limited to) gizzard plates and shell morphology, we have been able consistently to distinguish species within the *aperta* clade. Our cladistic analysis does not fully resolve the phylogeny of the clade, but it does demonstrate monophyly. Thus, the phylogenetic results combined with our anatomical descriptions clearly indicate that several species comprise the *aperta* clade.

Other large clades are clearly monophyletic, although Bremer support values are low. The fact that morphological characters alone do not provide a robust phylogeny strongly suggests that additional phylogenetic studies of *Philine* should include molecular phylogenetic data.

The form of the shell has traditionally been used to subdivide the genus *Philine* into different genera. For example, *Laona* A. Adams, 1865, for *Laona zonata*, A. Adams, 1865, was known only from a shell. Later, Pruvot-Fol (1954) included species in this genus that lacked gizzard plates. Later authors (Rudman, 1972b; Marcus, 1974; Gosliner, 1980, 1988) concluded that these genera are artificial and unnecessary. The present study sheds additional light on these issues. The species included in *Laona*, which lack gizzard plates, form a clade in the present analysis. However, recognition of *Laona* as a distinct taxon renders *Philine* paraphyletic. The same is true for *Spiniphiline* Gosliner 1988. *Spiniphiline* was erected to accommodate a species with several autapomorphic features, most notably spines on the shell. Nevertheless, *Spiniphiline* is nested within *Philine*, and its separation again makes *Philine* paraphyletic. Maintenance of these taxa serves no useful purpose, and these taxa should be regarded as synonyms of *Philine*, especially in light of the fact that the majority of Philinidae are still known only from shells and that our phylogeny has little Bremmer support. Subsequent revision of classification and nomenclature is necessary at some point, but it is premature to consider genera other than *Philine*, given the amount of missing data for the majority of its constituent species.

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